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Trophic Dynamics and Cyanobacteria Blooms In Shallow Eutrophic Bays Of Lake Champlain

Rebecca Michelle Gorney
University of Vermont, rgorney@uvm.edu

TROPHIC DYNAMICS AND CYANOBACTERIA BLOOMS IN SHALLOW EUTROPHIC BAYS OF LAKE CHAMPLAIN

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Rebecca M. Gorney

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Dissertation Examination Committee:

_____ Advisor
Mary C. Watzin, Ph.D.

_____ Committee
J. Ellen Marsden, Ph.D.

_____ Committee
Donna L. Parrish, Ph.D.

_____ Committee
Jason D. Stockwell, Ph.D.

_____ Chairperson
Ruth M. Mickey, Ph. D.

_____ Dean, Graduate College
Cynthia J. Forehand, Ph.D.

Date: March 24, 2014

ABSTRACT

This study was conducted to evaluate the relative roles of trophic dynamics and nutrient concentrations in the development of cyanobacteria blooms. The motivation for this research was to gain insights into how food webs respond to ecosystem-scale changes, using Lake Champlain as a case study. I sought to link field-based observations with experimentally derived data on mechanisms to better understand the processes that drive cyanobacteria blooms. My research addressed three specific topics: (1) associations among phytoplankton and nutrient concentration trends over time, (2) the impacts of planktivory by invasive fish on the ambient zooplankton community, and (3) the role of herbivore zooplankton grazers in determining the composition of the phytoplankton community.

I found little evidence of a strong association between nutrient concentrations and phytoplankton community composition during summer months in shallow bays of Lake Champlain prone to annual cyanobacteria blooms. Fish diet analysis indicated that invasive white perch (*Morone americana*) and alewife (*Alosa pseudoharengus*) selectively graze on large zooplankton, which has likely led to substantial declines in zooplankton biomass. I used these results to inform the design of a mesocosm study, which tested the effects of zooplankton grazing on phytoplankton and provided support for the theory that large zooplankton grazing pressure changes the size structure, abundance and composition of phytoplankton. High nutrient concentrations support increased levels of ecosystem productivity, but cascading trophic dynamics are additional forces that are likely contributing to the determination of phytoplankton community composition. Collectively, my research suggests that in shallow bays of Lake Champlain, selective grazing by invasive planktivorous fish is shifting the size structure of the zooplankton grazer community and has likely contributed to conditions that favor dominance by cyanobacteria in summer.

DEDICATION

This finished work is dedicated in loving memory to my sister, Rachel Miriam Gorney.

Everyday single day I miss your caring guidance and support.

I miss you with my whole heart.

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CHAPTER 1: COMPREHENSIVE LITERATURE REVIEW

1.1. Introduction

Anthropogenic activities have impacted ecosystem structure and function in nearly every biome on earth. Most aquatic ecosystems worldwide have declined in ecological integrity and our freshwater resources are threatened (Schindler 2006, Søndergaard *et al.* 2007). Lakes are clearly bounded systems and have similar food web structures worldwide so they are excellent systems in which to study the impacts of land use change and pollution. Three of the most common sources of impairment to aquatic ecosystems in the United States include: the degradation of physical structure, nutrient inputs, and the spread of invasive species (U.S.EPA 2009). When multiple factors converge on a single body of water, the interacting ecological impacts can be a challenge to unravel. Understanding and managing current threats to freshwater ecosystems requires a multi-disciplinary approach (Ricciardi and Rasmussen 1998, Schindler 2006). Humans depend on freshwater for drinking water, transportation, recreation, and food resources so protection of these habitats is a major focus for land managers and biologists.

Increases in aquatic nutrient concentrations lead to eutrophication and reductions in water quality. Despite extensive and expensive efforts, it is difficult to shift changes in lake conditions once deviations from historical conditions have occurred (Scheffer *et al.* 1997, Carpenter 2005, Schindler *et al.* 2008). The deterioration of previously stable conditions that follows eutrophication will lead to alternate states in the chemical, physical, and biological structure of a lake. Common changes include:

decreased water clarity, increased sedimentation, higher pH, the potential for anoxic conditions, and internal loading of nutrients from the sediment (Jacoby *et al.* 1982, Carpenter 2005, Schindler 2006). Higher productivity is expressed as increases in algal, zooplankton, and fish biomass (Scheffer and van Nes 2007). The community composition of each of these groups can be drastically altered from pre-eutrophication conditions.

An additional impact of anthropogenic changes in the landscape is artificial connections of water bodies, which increases the likelihood of invasive species spread and establishment (Rahel 2002). Lakes are increasingly susceptible to invasion by non-native species because of alterations in competitive interactions throughout the food web that result from the eutrophication process (Ricciardi 2001, Tilman 2004).

To evaluate driving factors that influence food web structure in lakes, studies have generally followed two separate lines of inquiry, so called "top-down" and "bottom-up" approaches (Carpenter and Kitchell 1992, Polis and Strong 1996). The first originated in observational studies of community interactions among fish, zooplankton, and phytoplankton as drivers of food web structure (Brooks and Dodson 1965, Carpenter *et al.* 1985). Experimental top-down studies test hypotheses from the perspective that it is the primary and secondary consumers that influence rates of primary productivity and algal community composition in lakes (Mazumder and Lean 1994, Vanni *et al.* 1997). The top-down paradigm in lakes was perpetuated in part by the promise of biomanipulation, the direct management of fish populations as a method to alleviate algal blooms associated with eutrophication (Carpenter *et al.* 1985, Leibold *et al.* 1997). Overall, efforts to control lake food webs by intentional fish removals or additions have

not been highly successful or long lasting (McQueen *et al.* 1989, DeMelo *et al.* 1992, Carpenter *et al.* 1996).

The second line of inquiry addresses nutrient concentrations and stoichiometry as drivers of food web structure in lakes. Bottom-up studies test nutrient concentrations and availability as influences on phytoplankton community composition (Reynolds 1999, Smith and Bennett 1999) and on higher trophic levels (Mazumder and Lean 1994, Demott *et al.* 2004). The density of colonial, grazing-resistant phytoplankton such as cyanobacteria has been strongly linked to nutrient supply and physical lake conditions in both observational and experimental contexts (Gliwicz 1990, Dokulil and Teubner 2000, Paerl *et al.* 2001, Michalak *et al.* 2013). Reductions in nutrient concentrations, particularly phosphorus, in aquatic systems is the most common management action prescribed to control the frequency and intensity of algal blooms (Conley *et al.* 2009, Schindler 2012), however, the presence of high concentrations of nutrients alone does not guarantee that cyanobacteria blooms will occur (Jeppesen *et al.* 1997, Elser 1999).

Studies that effectively combine bottom-up and top-down paradigms for an integrated, management-oriented and comprehensive approach are not common (Vanni and Layne 1997, Carpenter *et al.* 2001). Distinctions between the two perspectives are somewhat artificial because the phenomena they describe are not mutually exclusive (McQueen *et al.* 1989). More likely, there is constant dynamic feedback and interactions between consumers and their resources that determine community structure in lakes (Vanni *et al.* 1997, Carpenter *et al.* 2001, Shurin *et al.* 2002, Paerl and Paul 2012). The view of lake food webs as tidily fitting into distinct trophic levels largely ignores the

substantial complexity in a lake related to seasonal nutrient fluxes, climactic variability, indirect trophic interactions, and the role of the bacterial and detrital communities (Polis and Strong 1996, Schindler 2006).

The interactions among eutrophication, trophic dynamics, invasion by exotic species, and phytoplankton community structure are not well documented in one of the largest lakes in the United States, Lake Champlain. In this comprehensive review, I have summarized literature on these topics to provide a synthesis of current knowledge and the gaps in our understanding that still remain unanswered.

1.2. Eutrophication

The consequences of human-induced nutrient inputs to lakes were recognized long before the term eutrophication was coined. Increased algal growth, seasonal fish kills, and excessive macrophyte growth are just a few examples of easily observed evidence that a lake has become eutrophic. The causes of this ecological degradation were not firmly established in the public awareness until late in the 20th century (Schindler 2006). Some additional ecological consequences of eutrophication include: increases in pH caused by high rates of photosynthesis, high turbidity as a result of algal blooms or sedimentation, a loss of native biodiversity and seasonal declines in dissolved oxygen availability (Schindler 2006, Heisler *et al.* 2008). Eutrophic lakes frequently have reduced recreational value because of algal scums, odor problems, or dense macrophyte beds (Paerl 1996, Scheffer and van Nes 2007), so is was a high interest in discovering the causes of these problems. Beginning in the 1970s, David Schindler and others conducted whole lake experiments at the Experimental Lakes Area in Ontario, Canada to evaluate

the role of nutrients in ecosystem-level changes in lakes. Their studies and others isolated phosphorus (P) from carbon (C) or nitrogen (N) as the main nutrient limiting primary production in most lakes (Schindler 1977, Carpenter *et al.* 1996, Schindler 2012).

Following the establishment of excess P as the primary cause of eutrophication, extensive efforts have been put into place in the United States to manage nutrient sources to aquatic ecosystems (Schindler 2006, Conley *et al.* 2009). The passage of the Clean Water Act, bans on P additions to detergents and improvements in wastewater treatment have led to substantial reductions of point source loading of P to lakes (Schindler *et al.* 2008). Despite these efforts, nutrient enrichment is currently the third highest relative risk to biological condition for lakes in the United States, behind habitat loss and declines in habitat complexity (U.S.EPA 2009). Best Management Practices and requirements to meet established Total Maximum Daily Load plans are commonly implemented regulatory tools geared towards improving ecosystem health in lakes, though non-point sources of nutrients remain difficult to control, particularly in agricultural regions (Schindler *et al.* 2008, Conley *et al.* 2009). Interactions between climate and agricultural practices have been implicated for recent record-setting cyanobacteria blooms in Lake Erie (Michalak *et al.* 2013)

Regardless of controls on the rates of allocthonous nutrient input to eutrophic ecosystems, several autocthonous processes at the bottom of the lake will release additional dissolved nutrients directly into the water column (Søndergaard *et al.* 2003). These processes, collectively termed internal loading, include chemical and biological reactions that occur in both aerobic and anaerobic conditions at and just below the

sediment-water interface (Jacoby *et al.* 1982, Søndergaard *et al.* 2001). Internal loading of P is influential in maintaining a eutrophic state and fueling algae blooms. Several examples of the variety of processes that occur include: phosphate (PO_4) release from iron compounds in low redox conditions, bacterially mediated release of PO_4 as a consequence of the decomposition of organic matter, and release of nutrients bound to sediment particles when they are suspended into oxygenated water through wind action or bioturbation (Søndergaard *et al.* 2001). Additional biogeochemical reactions that lead to internal nutrient release are triggered by changes in pH, temperature, light, or the presence of macrophyte beds (Schindler 2006). It is difficult to accurately measure rates of internal loading and we do not fully know the proportional use of nutrients derived from internal versus external loading in the development or support of algae blooms (Søndergaard *et al.* 2003, Hambright *et al.* 2007b, Schindler *et al.* 2008). Non-linear community responses to reductions in loading suggest that externally derived nutrient inputs alone do not control algal productivity (Scheffer *et al.* 2001, Smayda 2008, Brauer *et al.* 2012).

Shallow lakes or bays are highly susceptible to rapid eutrophication (Romo *et al.* 2013) and they are particularly suitable for identifying interactions and trophic feedback mechanisms that can determine phytoplankton community composition (Jeppesen *et al.* 1997). The roles of wind-driven mixing, climate variations, light penetration, and water temperature are more influential to the ecology of shallow systems than to deeper systems (Scheffer and van Nes 2007, Kosten *et al.* 2012). High sediment to water surface ratios and warm water temperatures can lead to higher rates of internal loading, in part

because the sediments are within the photic zone (Søndergaard *et al.* 2003). Shallow systems are also more susceptible to large-scale perturbations such as climate change, invasion by alien species and fluctuations in nutrient inputs (Scheffer and van Nes 2007, Heisler *et al.* 2008). The ratio of watershed size to lake size is also an important factor in determining the influence of nutrient inputs to lake trophic status (Søndergaard *et al.* 2001)

Degradation of lakes can lead to drastic switches in ecological state rather than smooth, incremental responses to changes in climate, nutrient concentrations, habitat quality, or biodiversity (Scheffer *et al.* 2001). Eutrophic lakes are characterized by a process called hysteresis, in which an inherent stability slows the process of ecosystem change to or from a stable state (Scheffer *et al.* 1997, Carpenter *et al.* 2008). The classic model of these transitions among alternative stable lake states is the switch from a dense macrophyte-low turbidity lake to a dense algae-high turbidity lake following increases in TP or changes in the fish community (Scheffer *et al.* 1997, Ibelings *et al.* 2007). Climactic, physical, or chemical variables can change incrementally over time before a finally leading to a change in state that occurs on a relatively short time scale (Scheffer and Carpenter 2003).

Upon a change in state and passing a threshold of nutrient concentrations, simply reducing nutrients is usually insufficient to restore previous conditions (Søndergaard and Jeppesen 2007). In several restoration efforts, nutrient concentrations had to be lowered to less than the original threshold that brought about the change in state in the first place before any significant improvements in condition were documented

(Scheffer *et al.* 1997, Scheffer and Carpenter 2003, Ibelings *et al.* 2007). Sometimes several decades must pass following a reduction in external loading rates before water column nutrient levels remain consistently lower and productivity levels stabilize (Scheffer and van Nes 2007, Søndergaard *et al.* 2007).

Restoration of previous conditions requires attention to mechanisms related to the food web in addition to nutrient concentrations (Elser 1999, Scheffer *et al.* 2001, Schindler 2006, Paerl and Paul 2012). The community composition of fish, zooplankton, and phytoplankton varies substantially across different lakes, so interactions between nutrient concentrations and trophic structure will differ as well. The unique combinations of watershed characteristics, climate, and biota of each lake warrants research, monitoring, and management plans be tailored to the specific features of each lake on a system-specific basis (Reynolds 1998, Dokulil and Teubner 2000, Kosten *et al.* 2009, Paerl and Paul 2012).

Global climate change is likely to exacerbate the consequences of eutrophication and shift the timing of lake processes in unpredictable ways (Winder and Schindler 2004, Kosten *et al.* 2012). Seasonal fluctuations in zooplankton and phytoplankton communities might simply occur earlier in the year and remain in step (Hansson *et al.* 2013) or become out of sync and lead to substantial changes in trophic dynamics (Wagner *et al.* 2013). Spring diatom blooms, fish spawning patterns, and clear water phases caused by zooplankton grazing are all linked to several ecosystem processes that will be impacted by climate warming; new outcomes are probable but difficult to predict (Winder and Schindler 2004, Scheffer and van Nes 2007, Kosten *et al.* 2012). Increased

inter-annual variability in temperature and precipitation are likely to increase cyanobacteria blooms (Scheffer and van Nes 2007, Paerl and Huisman 2009, Carey *et al.* 2012, Paerl and Paul 2012). The ability to reduce bloom occurrence by lake management actions such as reductions in nutrient concentrations, in lake manipulations will become more challenging (Paerl and Huisman 2008, Kosten *et al.* 2012, Moss 2012).

Eutrophication of lakes is widespread but there are dynamic ecological processes within them that are not well understood. Variation in phytoplankton community composition has been widely studied, but no consensus has been reached as to why some taxa of phytoplankton dominate in one year and not another (Elser 1999, Scheffer *et al.* 2003, Schindler *et al.* 2008). Experimental and observational studies have demonstrated that the strength of the link among trophic levels is highly variable among eutrophic lakes and warrants further study (Brett and Goldman 1996, Hambright *et al.* 2007b, Carpenter *et al.* 2008).

1.3. Trophic Ecology

The earliest studies of ecology focused on energy movement through the food chain and how communities at several levels were dependent on one another. Energy transfer from producers to consumers and secondary consumers connects flora and fauna through dynamic interactions among trophic levels (Lindeman 1942). Growth and biodiversity at each trophic level is, in part, limited by energy availability (Polis and Strong 1996). In 1959, Hutchinson posed the then novel and now oft-tackled research question, "Why are there so many kinds of animals?" (Hutchinson 1959). He posed challenges to future scientists to uncover the ecological drivers of biodiversity. His early

insights on the potential contributions of both competition and environmental conditions in determining biodiversity have been supported through years of research. The study of how species with similar niche requirements are able to coexist and how abiotic attributes of the environment play a role in the structure of food webs remains a key focus in community ecology (Polis and Strong 1996, Tilman 2004).

In the 1960s and 1970s rapid advancements in understanding of both terrestrial and aquatic trophic ecology occurred as researchers worked to determine the relative importance of biotic and abiotic factors in driving species diversity and geographic distributions (Hairston *et al.* 1960, Connell *et al.* 1975, Pimm and Lawton 1977). The role of energetics in food webs was largely ignored in favor of experimental testing of concepts based on Lotka-Volterra models of species interactions (Paine 1980, Brown 1981, Scheffer *et al.* 2003). However, observational studies played a large role in the development of the theories and paradigms of trophic interactions in aquatic systems (Brooks and Dodson 1965, Smith 1970, Carpenter *et al.* 1985).

The relative influences of competition and predation in shaping food web structure were tested extensively and led to the development two key theoretical frameworks about trophic interactions that continue to shape the field of trophic ecology today. First, the trophic cascade concept describes the reciprocal effects of predator and prey interactions and alterations in productivity or abundance of populations across more than one trophic level (Paine 1980, Carpenter *et al.* 1985, Brett and Goldman 1997). Secondly, the keystone species concept suggests that some predators have a disproportionately large role in ecosystem function (Paine 1969, Power *et al.* 1996). Both

concepts came out of aquatic fields of study but have been expanded to terrestrial ecosystems as well (Pace *et al.* 1999, Polis *et al.* 2000).

Removal or additions of top predators, which are often keystone species, can lead to long-term change or regime shifts in lake food webs (Scheffer and Carpenter 2003, Carpenter *et al.* 2008, Estes *et al.* 2011). Cascading trophic interactions that result from perturbations at the top of the food chain can change system-wide productivity and functionality (Ellis *et al.* 2011). The loss of a top predator fish in a lake can lead to a proliferation of planktivorous fish, suppression of herbivore grazers, and increased growth of primary producers (Carpenter *et al.* 1985, Jeppesen *et al.* 1998).

Trophic levels moderate productivity in nutrient poor and nutrient rich systems, but the degree of control on the producer level depends on the presence of top predators (Hairston *et al.* 1960, Oksanen *et al.* 1981, Mazumder 1994). The length of the food chain is key for predicting what is controlling the abundance of primary producers. The difference between even and odd numbered food chain lengths can have consequences on many aspects of ecosystem structure and function (Power 1992, Polis and Strong 1996). Food chain models and empirical evidence from many temperate lake ecosystems indicates that algal biomass response to nutrient availability will be stronger in odd-link (3 or 5) than even-link systems (Jeppesen *et al.* 1997, Carpenter *et al.* 2001). The presence of a fourth, top predator trophic level, usually piscivorous fish in lakes, can mediate the effects of eutrophication.

The intertwined nature of bottom-up and top-down influences is clearest in species-rich communities, such as lake zooplankton and phytoplankton (Strong 1992).

There are several hypotheses that address why trophic cascades are strongest in aquatic systems (Power 1992, Shurin *et al.* 2002). Compared to terrestrial ecosystems, aquatic primary producers lack large, highly developed woody structures and therefore there is a larger proportion of the primary production that is edible and energy is more efficiently transferred among trophic levels (Shurin *et al.* 2002). A highly linked transfer of energy leads to a increased sensitivity to species addition or removal in aquatic ecosystems (Strong 1992), which is further enhanced in eutrophic conditions (Jeppesen *et al.* 1997, Vanni *et al.* 1997).

In a direct application of the principles of trophic cascades, biomanipulation has been suggested as a method to control eutrophication. Fish populations are either stocked or removed as part of a strategy to reduce algal densities (Carpenter *et al.* 1985). By manipulating the length of the food chain or number of trophic levels and leveraging cascading trophic interactions with zooplankton, temporary reductions in algal blooms are possible (Søndergaard *et al.* 2007). The lack of long-term success of these tactics has led to a shift in focus to control of nutrients alone or integrated efforts that address both nutrient and trophic dynamics (DeMelo *et al.* 1992, Elser 1999, Carpenter *et al.* 2001).

Researchers have attempted to parse out the relative strength of bottom-up and top-down interactions by conducting controlled experiments in mesocosms or enclosures (Brett and Goldman 1996, Vanni *et al.* 1997, Hambright *et al.* 2007b, Rondel *et al.* 2008). Controlled experimental manipulations of nutrients, grazers, or higher trophic levels (i.e., fish) can increase understanding of the mechanisms that cause trophic cascades. In a meta-analysis of 54 enclosure and lake experiment studies, Brett and Goldman (1996)

confirmed that trophic cascades do occur in lakes. In nearly all of the studies, high levels of planktivorous fish and low levels of zooplankton led to higher biomass of algae, but the strength of the interaction was inconsistent. In two thirds of the studies, the phytoplankton response to zooplankton manipulations was weak, while in the remaining third it was strong (Brett and Goldman 1996). The implications are that in some scenarios phytoplankton response to trophic changes is more dependent on variables other than zooplankton grazing (Brett and Goldman 1997, Vanni and Layne 1997). There are likely to be species and site-specific aspects to this association that are not known and are difficult to predict because of complex interactions among many variables (Jeppesen *et al.* 1997, Schindler 2006, Paerl and Paul 2012). Further study is needed into the role of zooplankton grazing in the determination of the structure of phytoplankton community composition (Elser 1999, Schindler 2006). This knowledge is especially valuable for the development of management plans for lakes prone to potentially toxic cyanobacteria blooms.

Top-down studies in lakes have focused on herbivorous zooplankton and fish predators as determinants of food web structure through selective consumption and predator-prey feedback loops that lead to long-term changes in all trophic levels (Hambright *et al.* 2007b, Palkovacs *et al.* 2008, Wang *et al.* 2010). Zooplankton and fish in eutrophic lakes can alter water column nutrient recycling rates (Vanni and Findlay 1990, Kraft 1993, MacKay and Elser 1998). Large zooplankton species such as *Daphnia* have higher proportions of P in their body tissue than smaller cladocerans such as *Bosmina* (Vanni and Layne 1997, Demott *et al.* 2004). The storage of nutrients in

zooplankton biomass reduces the amount available for phytoplankton uptake (Sterner 2008). Hence, when a lake undergoes a shift in zooplankton community composition towards smaller zooplankton species, increased algal growth can be partly attributed to this newly available pool of P (Hambright *et al.* 2007b). Fish, especially dense populations of planktivores in eutrophic lakes, will also add to the pool of algal available P via direct excretion and for bottom feeders, bioturbation of the sediments (Vanni and Layne 1997).

There is evidence that the role of higher trophic levels in biogeochemical cycling rates in lakes occurs at larger spatial scales than was previously assumed (Schindler 2006, Elser *et al.* 2007, Sterner 2008). While empirical accounts of these indirect impacts from small-scale experiments is valuable, they are not easily scaled up to whole lake ecosystems (Hambright *et al.* 2007a, Spivak *et al.* 2011). A more effective strategy to study trophic processes in lakes is to observe conditions in the lake itself and pair these with manipulative experiments (Eriksson *et al.* 2009, Palkovacs and Post 2009). Experiments allow for the control of individual variables and for researchers to assess the role of bottom-up or top-down processes separately (Sarnelle 1992, Vanni and Layne 1997). Identification of the relative importance of indirect and direct mechanisms by which trophic structure controls lake nutrient cycling is valuable to the formation of effective management plans and for ecosystem decision making (Lindenmayer and Likens 2010). For example, trophic dynamics can mediate the success of reductions in nutrient inputs as a lake restoration strategy (Jeppesen *et al.* 1997).

Unanswered questions remain about trophic dynamics in eutrophic lakes. For

example, we do not fully know the relative strength of consumer and resource control in pelagic food webs (Paerl and Paul 2012) or how trophic dynamics respond to eutrophication under different food-web configurations, such as following the establishment of invasive species. In Lake Champlain, several changes in trophic structure have occurred in recent years (Couture and Watzin 2008, Mihuc *et al.* 2012). Following invasion by alewife and white perch, substantial reductions in large zooplankton in the shallow bays of the lake could promote algae blooms and the dominance of potentially toxic cyanobacteria by reducing grazing pressure or altering nutrient availability rates and ratios. Controlled testing of the role of zooplankton grazing should be used to assess specifically how large zooplankton grazing affects the phytoplankton community composition in this system.

1.4. Invasive Species Ecology

The ecological impacts of invasive species on native trophic structure can have long-term deleterious impacts in aquatic ecosystems (Ricciardi and Rasmussen 1998). Humans have been implicated in most aquatic invasions in modern history (Mills *et al.* 1993, Søndergaard and Jeppesen 2007). Ballast water from shipping vessels, navigation canals, and attachment to small watercraft are a few of the most common routes for the spread of plant and animal species into waters in which they were previously absent (Rothlisberger *et al.* 2010).

Ricciardi and Rasmussen (1998) outlined several attributes of successful aquatic invasive species that include: high reproductive capacities, broad diets (opportunistic feeding), and wide environmental tolerances. Growth rates of invasive species in novel

systems are related to resource availability, the presence of natural predators, and habitat availability. The success of invasive species is also intimately linked with their ability to exploit unfilled ecological niches (Ricciardi 2001, Sakai *et al.* 2001). The analysis of a successful species invasion must incorporate the study of the ecology of the invasive species itself, impacts on the native community of both prey, competitors, and potentially farther reaching ecosystem-level impacts (Sakai *et al.* 2001, Shea and Chesson 2002). In Lake Huron, an analysis of a long-term dataset revealed complex interactions between zebra mussels and cyanobacteria. Zebra mussels (*Dreissena polymorpha*) consumed other competing phytoplankton, reduced the populations of zooplankton grazers, and selectively avoided consumption of colonial cyanobacteria, leading to a high success rate of *Microcystis* despite reductions in ambient nutrient concentrations (Fishman *et al.* 2010).

With each new regional expansion of a species, there remains some degree of uncertainty as to the regional impact and potential interactions with native biota (Ricciardi and Rasmussen 1998). Lakes provide a convenient ecological unit within which study invasive species and their spread. Studies of the impacts of recent invasions are comparable to unplanned ecosystem-level experimental manipulations. New invasions provide opportunities to test hypotheses drawn from the impacts of earlier invasions in other lakes (Sakai et al. 2001).

There has been extensive research conducted on invasive species in the Great Lakes where ecological and economic impacts have been substantial (Stewart *et al.* 2010, Guzzo *et al.* 2013). Many invasive species have little to no deleterious impact on lake

food webs, but for others there has been a disproportionately strong effect that can drastically alter ecosystem health. Invasions of non-native fish have led to changes in the phytoplankton, zooplankton and fish communities, particularly in Lakes Ontario and Erie (Mills *et al.* 1993, Stewart *et al.* 2010). Relationships between invaders and native species usually strongly benefits the invader and with continued rates of new species discovery, the effects of invaders continue to expand in the Great Lakes (Ricciardi 2001). Interactions among invasive species have created food webs that bear little resemblance to earlier conditions (Mills *et al.* 1993).

Several invasive species have entered the Great Lakes through canals that artificially connect previously distinct waterways (Mills *et al.* 1993). Canals have also served as a vector for invasion from the Great Lakes into other large lake ecosystems. While connectivity to Lake Champlain by the Champlain and Erie Canals has been an possible vector for invasion, the rate of discovery of new species of fish, mollusks, and invertebrates into Lake Champlain remains lower than that of the Great Lakes (Marsden and Hauser 2009). Additionally, the impacts of some invaders in Lake Champlain have not necessarily followed predictions that were formulated based on patterns observed in the Great Lakes (Miller and Watzin 2007, Simonin *et al.* 2012).

Alewife (*Alosa pseudoharengus*) are one of the most recent invaders into Lake Champlain (first documented in 2003) that may have a long-term impact on lake ecology (Marsden and Hauser 2009). Alewife are an anadromous species, native to the Atlantic Ocean. They are obligate planktivores that prefer to consume zooplankton throughout their life history (Lazzaro 1987). The introduction of alewife into the Great Lakes has

been associated with substantial changes to fish, invertebrate, and phytoplankton community composition, particularly in Lakes Huron, Michigan, and Ontario (Wells 1970, Eck and Wells 1987, Madenjian *et al.* 2008). The species was first detected in Lake Ontario as early as 1873, introduced by either unintentional introduction or passive spread of the species from the Hudson River drainage (Scott and Crossman 1973, Mills *et al.* 1993). Daniels (2001) outlines a history of the contradictory theories of how alewife was introduced into Lake Ontario and other New York lakes. Claims include stocking, the Erie Canal, and natural movement through river systems such as the Susquehanna and Saint Lawerence (Daniels 2001).

Regardless of how alewife entered Lake Ontario, with the completion of the Welland Canal, alewife spread to the other Great Lakes and established quickly, reaching very high abundances in some years (Scott and Crossman 1973, Eck and Wells 1987). Alewife were present in large numbers in lakes Ontario, Michigan, and Huron by the middle of the twentieth century. Following establishment of alewife, declines in native planktivorous fish occurred rapidly. Eventually, declines in nearly every common native fish species have been attributed at least in part to alewife (Smith 1970, Madenjian *et al.* 2008).

In Lake Michigan, size selective predation by alewife led to substantial declines in the largest zooplankton taxa less than two decades after alewife were initially found in the lake (Wells 1970). The success of alewife in the Great Lakes has been attributed to high fecundity, strong preference for the abundant large zooplankton, and out-competing native fish species through physical displacement, competition for prey, and consumption

of their eggs (Madenjian *et al.* 2008). The establishment of alewife in Lake Champlain may also lead to declines in large zooplankton and native fish (Marsden and Hauser 2009). Large cyclical die-offs of alewife and the development of thiamine deficiency disorder in salmonids that consume alewife are also possible (Scott and Crossman 1973, Brown *et al.* 2005).

White perch (*Morone americana*), an estuarine species that is also native to the Atlantic Ocean, have also caused widespread deleterious impacts in the Great Lakes (Mills *et al.* 1993). White perch spread from first detection in the Lake Ontario watershed in 1950 to all five lakes (Scott and Crossman 1973). It became the dominant fish species in the Bay of Quinte within one decade (Hurley 1992). White perch have been linked with declines in native fish species and zooplankton abundance, particularly in Lakes Erie and Ontario (Schaeffer and Margraf 1987, Hurley 1992, Guzzo *et al.* 2013). White perch have spread into many other inland lakes in the eastern United States and Canada (Prout *et al.* 1990, Feiner *et al.* 2013). White perch entered Lake Champlain in the mid 1980s through the Champlain Canal and made their way north, establishing populations throughout the lake in areas that were suitable to their broad habitat requirements (Hawes and Parrish 2003). They have plastic preferences in both lifestyle and diet, characteristics that make them highly successful invaders (Hurley 1992, Kerr and Secor 2012). White perch have been commonly observed to consume zooplankton when available, but their diet preferences are substantially broader than an obligate planktivore such as alewife (Schaeffer and Margraf 1987, Prout *et al.* 1990, Gopalan *et al.* 1998).

It is unknown whether the recent invasions by alewife and white perch into Lake

Champlain will lead to similar outcomes as previous invasions in other lakes in the northeastern United States. The ecological impacts of both species are likely to increase in the future (Marsden and Hauser 2009, Mihuc *et al.* 2012) and warrants further study. Both alewife and white perch have the potential to impact the food web of the whole lake through the selective consumption of large zooplankton, other invertebrates, and eggs of native fish species (Carpenter *et al.* 2008, Madenjian *et al.* 2008). A study of white perch diet composition in Missisquoi Bay, Lake Champlain found that large zooplankton, such as *Daphnia* and *Leptodora*, were selectively consumed over other available zooplankton, such as copepods (Couture and Watzin 2008). The results of this zooplanktivory could be reduced biomass of large zooplankton, reduced grazing pressure on phytoplankton, and potentially increased algal blooms (Carpenter *et al.* 1985, Jeppesen *et al.* 1997, Elser 1999). In the same time frame that white perch have become established in Lake Champlain, the density of potentially toxic cyanobacteria blooms have increased but a link between the two remains to be demonstrated.

1.5. Phytoplankton Blooms and Ecology

Phytoplankton is a multi-phyletic group of microorganisms that are present in every marine and freshwater ecosystem. Competition, resource partitioning, grazing, and changing environmental conditions can all influence species survival (Scheffer *et al.* 2003). Diverse communities of phytoplankton observed in temperate lakes defy the predications of the competitive exclusion principle (Tilman 1982). Multiple species within a given body of water seem to have nearly identical nutrient and environmental requirements, which is the basis of Hutchinson's '*paradox of the plankton*' (Hutchinson

1961). The determination of how or why a particular type of phytoplankton dominates within a season or between years has been a challenging question to ecologists and some argue, one that still has not been adequately resolved (Scheffer *et al.* 2003, Roy and Chattopadhyay 2007). Ecological modeling and lab studies have demonstrated some of the potential mechanisms of coexistence among species but applying those results on an ecosystem scale remains challenging (Perruche *et al.* 2010, Brauer *et al.* 2012).

Predictions of annual algal community composition are of particular importance when it comes to management of harmful algal blooms (HABs), such as cyanobacteria. Because of high levels of unpredictability in phytoplankton community structure and a general lack of understanding of bloom development mechanisms, there is a need for continued study, particularly in cases where potentially toxic cyanobacteria blooms threaten human or ecological health of a lake ecosystem (Scheffer *et al.* 1997, Hyenstrand *et al.* 1998, Schindler 2006, Paerl and Paul 2012). HABs impact ecological health through the production of toxins and fish kills. They also reduce recreational values and increase human health risks (Chorus *et al.* 2000, Dokulil and Teubner 2000, Codd *et al.* 2005).

In shallow eutrophic lakes, the most common HABs are cyanobacteria. These autotrophic prokaryotic taxa are more similar to bacteria than other plants and once established as the dominant taxa in a lake, it is difficult to recover the native diversity of phytoplankton species (Scheffer *et al.* 1997, Roelke *et al.* 2007, Schindler 2012). Cyanobacteria blooms worldwide are usually dominated by the same taxa, commonly including the following genera: *Aphanizomenon*, *Anabaena*, *Oscillatoria*, *Microcystis*,

Planktothrix, and *Lyngbya* (Paerl 1996, Scheffer *et al.* 1997, Dokulil and Teubner 2000). Because many cyanobacteria have similar but not identical environmental requirements, predictions of which ones will be most prevalent in a body of water during a bloom are difficult (Sterner 1989, McCausland *et al.* 2002, Lürling *et al.* 2013).

Cyanobacteria have several physiological and ecological attributes that contribute to their competitive success over other types of phytoplankton. Several species of cyanobacteria can regulate their buoyancy, have superior ability for cellular storage of nutrients, avoid herbivores by producing toxins and size limitations, exploit ammonium-N, and out-compete other types of phytoplankton for trace elements (Hyenstrand *et al.* 1998). Some of the environmental conditions that provide cyanobacteria an advantage include: low N:P nutrient supply ratio, high light irradiance, low concentrations of CO_2, high water column stability, and warm temperatures (Hyenstrand *et al.* 1998, Paerl *et al.* 2001). Several studies have addressed how each of these mechanisms, individually and in combinations, correlates with the occurrence and duration of cyanobacteria blooms but the ability of researchers to predict precisely what triggers blooms remains elusive (Downing *et al.* 2001, Scheffer and van Nes 2007, Schindler *et al.* 2012). Evaluations of interactions among nutrient concentrations, the ratio of available N:P, light availability, and grazing-induced mortality have led to several hypothesized routes to bloom formation (Elser 1999, Dokulil and Teubner 2000, Huisman and Hulot 2005). Low N:P ratio, appears to be the best single predictor of cyanobacteria blooms in some studies (Smith 1983, Smith and Bennett 1999, Havens *et al.* 2003).

Resource ratio competition theory predicts that the outcomes of competition will

be determined by differential abilities to compete for important resources, so it has been appealing to link bloom development exclusively to nutrient concentrations or ratios (Tilman 1982, Tilman *et al.* 1986, Carey *et al.* 2012). Nearly all species of cyanobacteria are better competitors for nitrogen than other phytoplankton, so in conditions where dissolved forms of P are relatively highly available, this competitive advantage can contribute to dominance and bloom development (Smith and Bennett 1999, Paerl *et al.* 2001). However, numerous studies have demonstrated that there is not always a clear association between nutrient ratios and cyanobacteria dominance and that other factors interact with nutrient concentrations to impact the outcome of phytoplankton interspecific competition (Jensen *et al.* 1994, Downing *et al.* 2001, Scheffer *et al.* 2003).

In recent years, the analysis of large datasets from numerous lakes, new analytical methods, and dynamic modeling techniques have led to a broader understanding of the mechanisms that might lead to blooms beyond nutrient supply ratios (Downing *et al.* 2001, Brauer *et al.* 2012, Paerl and Paul 2012). Both experimental and observational studies have demonstrated that total nutrient concentrations (particularly TP), light availability, or total standing algal biomass can be better predictors of the likelihood of cyanobacteria dominance (Trimbee and Prepas 1987, Downing *et al.* 2001). Scheffer and van Nes (1997) evaluated 55 shallow lakes in the Netherlands and tested relationships among nutrients, light, and cyanobacteria bloom development. They found no relationship with nutrients and but instead found light levels to be highly significant, especially in scenarios with lower TP. Their explanation was that once blooms get started, the cyanobacteria shade out all other types of phytoplankton and create

conditions in which only they can survive. This hypothesis is supported by dynamic models in lakes with high nutrient concentrations (Brauer *et al.* 2012).

Conversely, top-down studies point to the role of food web dynamics in the determination of algal community structure (Stein *et al.* 1995, Jeppesen *et al.* 1997, Hambright *et al.* 2007b). In eutrophic systems, the addition of invasive planktivorous fish that graze selectively on large cladocerans can be the final tipping point to cyanobacteria dominance (Elser 1999). Declines in zooplankton biomass can tip the balance in favor of cyanobacteria dominance by reducing in grazing pressure on phytoplankton such as chlorophytes and through shifts in nutrient recycling rates by zooplankton and fish (Carpenter *et al.* 1985, Vanni and Layne 1997). Changes in phytoplankton community composition often occur in lakes where species invasions by fish or other predator trophic levels have altered the native zooplankton size structure and total biomass (Brooks and Dodson 1965, Vanni and Findlay 1990, Wang *et al.* 2010). Zooplankton consume some cyanobacteria, particularly when colony size is small (Gliwicz 1990). Recent evidence suggests that small zooplankton may consume cyanobacteria more than large zooplankton so cyanobacteria are an important part of the trophic structure within eutrophic lakes prone to blooms (Perga *et al.* 2013).

Since there remains uncertainty about the process of bloom development, the analysis of long term monitoring data can be particularly valuable to understand changes in phytoplankton community composition over time (Lovett *et al.* 2007, Roelke *et al.* 2007). Because of inter-annual variation in the seasonal timing of environmental factors that are relevant to bloom development, multi-year studies are particularly valuable to

detect long-term trends (Dokulil and Teubner 2000, Lovett *et al.* 2007). Long-term datasets from Lake Champlain have revealed an increased prevalence of cyanobacteria in shallow bays that have undergone recent rapid eutrophication (Smeltzer *et al.* 2012). Inter-annual variation in the composition, density, and duration of cyanobacteria blooms is substantial in several of the shallow bays (Watzin *et al.* 2012) making them good sites for additional studies of bloom dynamics.

1.6. Lake Champlain: Site Description and Recent Research

Lake Champlain is a deep, glacially carved lake bordered by Vermont, New York and Quebec, Canada (Figure 1.1). Following the retreat of glaciers 10,000 to 12,000 years ago, the lake fauna was re-colonized by species remaining in aquatic refugia through connections to the Hudson and Mohawk River drainages to the west, the St. Lawrence Valley to the north, and the Connecticut Valley to the east. The lake has a diverse assemblage of fish and invertebrates that reflects its unique biogeographic history (Marsden and Langdon 2012). It has a maximum depth of 122 m and a mean depth of 23 m with considerable variation in trophic state throughout the lake. Some sections are currently considered mesotrophic or oligotrophic (Main Lake) while others are eutrophic (South Lake, Northeast Arm, certain shallow bays), based on nutrient concentrations and algal community composition (Levine *et al.* 2012, Smeltzer *et al.* 2012).

The relatively forested landscape, minimal amount of industrial manufacturing, and low human population density are key reasons why Lake Champlain is less ecologically degraded compared to other large lakes in the United States (Marsden and Langdon 2012, Smeltzer *et al.* 2012). In recent decades species introductions have

increased and led to widespread impacts on the food web ecology that will likely continue as new species enter the system in the future (Marsden and Hauser 2009, Mihuc *et al.* 2012).

The largest ecological and economic impacts in Lake Champlain from invasive species have been caused by five plants and animals: water chestnut (*Trapa natans*), Eurasian water milfoil (*Myriophyllum spicatum*), purple loosestrife (*Lythrum salicaria*), zebra mussels, and alewife (Marsden and Hauser 2009). White perch is an additional invasive fish species that is widespread throughout Lake Champlain and may be causing trophic changes through the selective consumption of large zooplankton (Couture and Watzin 2008).

At the northeastern terminus of the lake, Missisquoi Bay is a large, shallow bay with surface area of 77.5 km^2; mean depth of 3 m; max depth of 4 m; and catchment area of 3,105 km^2 (Figure 1.1, Levine et al., 2012). The land use of the watershed is about 25% agriculture, which contributes about 70% of the annual P entering the bay (Troy *et al.* 2007). The Missisquoi Bay watershed contributes the highest nutrient loads of all of the sub watersheds of Lake Champlain. The bay is considered eutrophic with annual TP concentrations that have been gradually increasing since the 1980's to current annual mean values greater than 45 $\mu g\ L^{-1}$ (Smeltzer *et al.* 2012).

Paleolimnological evidence suggests that deforestation and the rise of agriculture that has occurred since Europeans settled in the area have led to increased eutrophication throughout the lake. The continued intensification of agricultural development in the Missisquoi Bay watershed since 1970 has contributed to increased

sediment input, higher nutrient loads, and a decline in water quality (Levine *et al.* 2012). Nutrient concentrations, phytoplankton, zooplankton, and fish communities have all changed substantially in the 40 years since a quantitative study identified the bay as "not highly productive" (Keen and Potash 1978, Smeltzer *et al.* 2012).

Missisquoi Bay has become a regional focus of ecological research, in part because of the high nutrient loads delivered to the main lake and because of the annual occurrence of dense, potentially toxic cyanobacteria blooms. Cyanobacteria has historically been present in the bay but it is only in recent decades that annual blooms with toxin levels that threaten human safety have been observed (Watzin *et al.* 2006, Smeltzer *et al.* 2012, Watzin *et al.* 2012).

In 1999, two dog deaths occurred from consuming lake water during an algae bloom in Lake Champlain. It is presumed that the deaths were the result of anatoxin present in an *Anabaena flos-aquae* bloom (Boyer *et al.* 2004). A tiered monitoring program was developed in 2003 to better understand the extent, composition, and toxicity of algal blooms throughout Lake Champlain with particular focus on Missisquoi, Saint Albans, and Burlington Bays (Watzin *et al.* 2006). The program was conducted from 2003-2012 and primarily served to inform public health officials and the general public about potentially toxic bloom events throughout the Vermont and New York areas of the lake (Watzin *et al.* 2012). Several other monitoring programs designed to collect data on physical, chemical, and biological variables throughout Lake Champlain have been in place since the 1960s. Most recently, the Long Term Monitoring Program maintains several permanent sampling stations throughout the lake. Data is collected through

partnerships between scientists and managers in Vermont and New York states, the province of Quebec, and the Lake Champlain Basin Program (Smeltzer *et al.* 2012).

Research topics addressed in Missisquoi Bay have included changes in the fish community, biogeochemical processes at the sediment water interface, phytoplankton community dynamics, phosphorus sources from the watershed, and others (Rogalus and Watzin 2007, Couture and Watzin 2008, Herbst *et al.* 2011, Smith *et al.* 2011, Ford 2012, Levine *et al.* 2012, Hart *et al.* 2013, Pearce *et al.* 2013). In the future, further high-resolution data on phytoplankton and biogeochemical processes that occur in Missisquoi Bay will be collected and analyzed in the context of adaption to climate change (EPSCoR 2013).

The Missisquoi Bay fish community has changed appreciably in roughly the same timeframe that the bay has become eutrophic. The bay once supported a robust population of whitefish (*Coregonus clupeaformis*) and likely other cold or cool-water fish. Extensive sampling suggested that whitefish no longer spawn in Missisquoi Bay, probably as a result of habitat alterations (Herbst *et al.* 2011).

In addition to whitefish, historically there were historically higher numbers of walleye (*Sander vitreus*) in Missisquoi Bay. Walleye densities were high enough to support a commercial harvest in the early 20th century, until populations declined around 1960 (Marsden and Langdon 2012). Community assessments conducted by the Vermont Department of Fish and Wildlife at Sandy Point in Missisquoi Bay have documented walleye abundance measured as catch per unit effort on an annual basis through the 1950s and 1960s, and then every five years, starting in 1985 (B. Pientka, *unpublished*

data). Current walleye densities are much lower than during the 1950s and 1960s (Marsden and Langdon 2012). The community assessments have also been valuable for documenting the spread and establishment of invasive fish species into Missisquoi Bay. White perch first appeared in the seining efforts in 2000, and by 2005 had increased substantially in relative abundance. Alewife were first collected in Missisquoi Bay in 2003 but did not first appear in seine samples until 2010 (B. Pientka, *unpublished data*).

The invasion of white perch into Missisquoi Bay prompted a study of diet composition and experiments that demonstrated their potential predation pressure on large zooplankton (Couture 2006). It is possible that size selective predation on large zooplankton by the fish is leading to trophic cascades. Lower biomass of large, herbivorous zooplankton reduces grazing pressure on phytoplankton and may interact with increased nutrient availability to lead to cyanobacteria blooms (Carpenter *et al.* 1985, Elser 1999). In Missisquoi Bay, declines in large zooplankton biomass in the ambient zooplankton community occurred coincident with selective feeding by white perch on those taxa (Couture 2006). Following invasion by both white perch and alewife, zooplankton size and biomass have declined throughout shallow bays of Lake Champlain (Mihuc *et al.* 2012), but no studies have yet addressed the potential for competition between these two species in Lake Champlain. The combined feeding activity of both species in Missisquoi Bay may continue to lead to a reduction in zooplankton grazing pressure on phytoplankton, which will lead to an increased likelihood of annual cyanobacteria blooms in Missisquoi Bay.

Mihuc *et al.* (2012) examined patterns in the zooplankton community

composition lake-wide from 1992-2010. They pooled data from multiple deep and shallow bays, including Missisquoi Bay, and evaluated trends since the start of long-term monitoring by the Vermont and New York Departments of Environmental Conservation. A reduction of large cladocerans and rotifers occurred in deep sites shortly after zebra mussels invaded. A decrease in the size of some zooplankton taxa was attributed to size selective feeding by alewife (Mihuc *et al.* 2012), but there currently is no published documentation on alewife diet in Lake Champlain.

Changes in the trophic dynamics of shallow lakes can interact with the availability of nutrients to support algae blooms (Elser 1999). N and P concentrations in lakes come from external loading from the watershed and internal loading from lake sediments (Scheffer *et al.* 1997, Søndergaard *et al.* 2001). We do not fully understand the partitioning of sources of nutrients that support algae blooms in Missisquoi Bay, such as whether they are from external inputs or internal loading. Electrochemical profiling in Missisquoi Bay has documented seasonal and diel fluctuations in the redox front at the sediment-water interface and increased P flux from the sediments during cyanobacteria blooms (Smith *et al.* 2011).

Reductions of sediment, nutrient and pollutant loads are the most common management actions taken for the management of eutrophic lakes (Carpenter *et al.* 2001, Conley *et al.* 2009, Elser and Bennett 2011). Many studies support an interdisciplinary approach to managing eutrophication in shallow systems using an adaptive management strategy (Schindler 2006, Scheffer and van Nes 2007, Conley *et al.* 2009). P loading from the Missisquoi Bay watershed has been increasing for about 30 years (Smeltzer *et al.*

2012), mostly from increases in agricultural fertilization application practices (Ford 2012). Given the long period of high nutrient inputs to the bay, internal loading and dissolved P release during low redox conditions are likely to continue for many years, even following a substantial reduction in incoming loads (Jeppesen *et al.* 1998, Søndergaard *et al.* 2003, Smeltzer *et al.* 2012).

1.7. Scope and Goal of this Study

The goal of my research was to link experimentally derived data on the mechanisms that support cyanobacteria blooms with field-based observations to better understand the patterns of abundance in shallow eutrophic bays of Lake Champlain. The body of this dissertation consists of three separate manuscripts. I examined 1) long-term patterns in phytoplankton community composition, 2) the selective consumption of zooplankton by two invasive species of planktivorous fish and 3) the response of phytoplankton to zooplankton grazing in experimental mesocosms. The material presented in this dissertation is inherently interdisciplinary in nature. The prominent themes include eutrophication, trophic dynamics, phytoplankton ecology, and invasive species ecology.

In the first study, I investigated the main seasonal and temporal variations in nutrient concentrations and phytoplankton community composition from 2003-2011 in two shallow eutrophic bays of Lake Champlain: Saint Albans Bay and Missisquoi Bay. I attempted to establish a link between the most common phytoplankton genera and nutrient concentrations during peak cyanobacteria bloom conditions. The aims were three-fold: (1) to define the seasonal patterns of nutrient concentrations, (2) to summarize

the phytoplankton community composition both seasonally and on an inter-annual basis, and (3) to evaluate whether the prevalence of major phytoplankton groups for each bay was related to nutrient variables.

In the second study, I conducted a diet analysis of two invasive fish species, white perch and alewife, in Missisquoi Bay to evaluate their impacts on the food web. Diet composition in Missisquoi Bay in 2010 and 2011 were compared to an earlier study conducted in 2005, prior to invasion by alewife (Couture and Watzin 2008). Changes in the ambient zooplankton community composition were compared using these data and historic records from 1976-77 (Keen and Potash 1978). The objectives were to (1) characterize the diet composition of adult white perch and adult alewife in 2010 and 2011, (2) describe changes in the ambient zooplankton community using historical and current composition data, and (3) evaluate the ecological impacts of coexistence of both fish species, particularly their selectivity among zooplankton from the ambient community.

The results of the diet study were used to formulate the design of my third study, a mesocosm experiment conducted on the shores of Missisquoi Bay. I evaluated the response of phytoplankton to manipulations of the zooplankton community. In mesocosms, I established treatments with enhanced or reduced quantities of large zooplankton for 10-day trials (July and August 2011, May 2012). The main question tested was how does biomass of large and small zooplankton sizes classes impact phytoplankton abundance and community composition. Collectively, these three studies explore both bottom-up and top-down processes that may be contributing to

cyanobacteria blooms in Lake Champlain.

Figure 1.1: Map of Lake Champlain, with insets showing regional location (left) and detail of Missisquoi Bay (right). Markers indicate the locations of UVM long-term phytoplankton monitoring sites in Missisquoi Bay. Red line indicates the US and Canada border.

CHAPTER 2: ASSESSMENT OF NUTRIENT TRENDS AND PHYTOPLANKTON COMMUNITY COMPOSITION WITHIN SHALLOW BAYS OF LAKE CHAMPLAIN

2.1. Abstract

As eutrophication and potentially toxic cyanobacteria blooms increase in occurrence and intensity worldwide, there is a growing interest in linking environmental factors and algal community composition. Monitoring programs created for assessing bloom conditions and protecting human health are valuable for the evaluation of long-term phytoplankton and nutrient trends. We used a monitoring dataset from Lake Champlain to explore whether these monitoring data might be valuable for suggesting mechanistic patterns that could help advance understanding about what drives potentially toxic cyanobacteria blooms. In this study, seasonal and interannual variation in nutrient concentrations and phytoplankton community composition from 2003-2011 were investigated in two shallow eutrophic bays of Lake Champlain. Associations between phytoplankton and nutrient concentrations during peak cyanobacteria bloom conditions were also explored. Phytoplankton cell counts, total phosphorus, total nitrogen, soluble reactive phosphorus, and dissolved inorganic nitrogen samples were collected from July to October in Saint Albans Bay and Missisquoi Bay on a twice monthly or weekly basis. The bays differed in their nutrient concentrations but were similar in seasonal patterns. Both bays were dominated by cyanobacteria but the generic composition differed with Missisquoi Bay dominated by *Microcystis* and Saint Albans Bay dominated by *Anabaena*. Redundancy analysis (RDA) indicated that the measured nutrient variables

did not predict phytoplankton community composition of either bay.

2.2. Keywords

Phytoplankton, Lake Champlain, monitoring program, cyanobacteria, phosphorus

2.3. Introduction

Temperate shallow lakes become eutrophic as a result of increases in nutrient inputs and can undergo substantial ecological shifts. Eutrophic lakes are characterized by high productivity, increases in pH as a result of high rates of photosynthesis, increases in turbidity, and rapid turnover of dissolved nutrients in the water column as they are readily taken up taken up by algae (Schindler 2006, Scheffer and van Nes 2007). Cyanobacteria blooms often dominate the phytoplankton community of temperate eutrophic lakes (Heisler *et al.* 2008). These ancient, cosmopolitan inhabitants of all aquatic ecosystems are far from benign players in lake food webs as they are capable of producing powerful toxins (Codd *et al.* 2005) and have been associated with declines in all other types of phytoplankton (Downing *et al.* 2001). In lakes that supply public drinking water, the risks associated with toxin-producing cyanobacteria include threats to public health, which warrants regular monitoring of algal densities (Chorus and Bartram 1999).

As eutrophication and potentially toxic cyanobacteria blooms increase in occurrence and intensity worldwide, there is a growing interest in linking environmental factors to long-term trends in phytoplankton community structure (Dokulil and Teubner 2000, Brauer *et al.* 2012). Cyanobacteria bloom dynamics have been related to nutrient concentrations, nutrient ratios, trophic interactions with zooplankton grazers, competition

for light, water temperature, water column stability, and available CO_2 (Hyenstrand *et al.* 1998, Elser 1999, Carpenter *et al.* 2001, Brauer *et al.* 2012). Conflicting results among studies indicates that there is not a clear consensus on the mechanisms that cause or perpetuate blooms. With the onset of climate change and warmer global temperatures, the dominance of cyanobacteria in shallow lakes is likely to continue to rise (Scheffer and van Nes 2007, Paerl and Huisman 2008, Kosten *et al.* 2012); therefore, a more complete understanding of bloom mechanisms is vital.

Long-term monitoring data helps to inform management decisions and can provide critical insights into trends in ecosystem processes (Lovett *et al.* 2007). Analyses of monitoring data can also help to generate new questions about ecological dynamics that can be tested experimentally (Lindenmayer and Likens 2010). Cyanobacteria bloom monitoring datasets provide rich information on phytoplankton community composition and associated environmental variables such as nutrient concentrations and physical parameters (Suikkanen *et al.* 2007). The temporal or spatial resolution of these environmental variables will vary by lake and might change from year to year (Scheffer *et al.* 2003, Roelke *et al.* 2007) but comprehensive datasets provide ecologists with the capability to look for trends or patterns that can advance our understanding of how eutrophication and cyanobacteria blooms function.

One such monitoring dataset was collected in Lake Champlain starting in 2003 as a result of increasingly common cyanobacteria blooms in several locations throughout the lake (Watzin *et al.* 2006). Lake Champlain lies on the border between Vermont and New York states and extends north into Quebec, Canada (Figure 2.1). The design of the

phytoplankton monitoring program in Lake Champlain was based on an "Alert Levels Framework" (Chorus and Bartram 1999) that triggers a graduated response to potentially harmful blooms based on the observation of potential toxin producers (Watzin *et al.* 2012). The program was conducted for nine years (2003-2011) and primarily served to inform public health officials and the general public about potentially toxic bloom events to protect drinking water supplies and recreational users of the lake (Watzin *et al.* 2012). Two shallow bays at the northern extend of the lake, Missisquoi Bay and Saint Albans Bay, were particularly prone to toxic cyanobacteria blooms throughout the monitoring program (Smeltzer *et al.* 2012, Watzin *et al.* 2012) and thus provide the richest data set.

Using the data from this monitoring program, we explored trends and patterns in the distribution of nutrients and phytoplankton in Missisquoi and Saint Albans Bays in Lake Champlain from 2003-2011. The aims were three-fold: (1) to define the seasonal patterns of nutrient concentrations, (2) to summarize the phytoplankton community composition both seasonally and on an inter-annual basis and (3) to evaluate whether the prevalence of major phytoplankton groups in each bay were related to nutrient concentrations. Our working hypothesis was that nutrient concentrations would have substantial different explanatory power and we predicted that it would differ between the two bays and among types of phytoplankton.

2.4. Methods

2.4.1. Study Sites and Sample Collection

Lake Champlain is a long, narrow lake with a maximum width of 20 km and a

length of 193 km. Missisquoi Bay is a shallow, eutrophic bay at the northern extent of the lake (Figure 2.1) and has the highest annual nutrient concentrations and the densest cyanobacteria blooms in Lake Champlain. Saint Albans Bay, which lies 25 km south of Missisquoi Bay (Figure 2.1), is a smaller, deeper bay also prone to periods of cyanobacteria blooms each summer. Nutrient concentrations are lower and cyanobacteria blooms have historically been less dense in Saint Albans Bay than Missisquoi Bay (Smeltzer *et al.* 2012, Watzin *et al.* 2012).

Phytoplankton monitoring in Lake Champlain was conducted according to a tiered monitoring and alert system previously described in detail (Watzin *et al.* 2006, Rogalus and Watzin 2007, Watzin *et al.* 2012). The program was designed to be an efficient way of monitoring cyanobacteria densities and cyanotoxins for the purpose of alerting public health officials of the risk of exposure to toxins, particularly microcystin (Watzin *et al.* 2006). Sample collections began each year in early June and continued until all potentially toxic cyanobacteria blooms had senesced, generally late October. Sampling frequency was tied to rapid assessment counts of potentially toxic cyanobacteria, advancing from twice-monthly to weekly as bloom conditions (> 4000 potentially toxic cells mL^{-1}) were observed (Watzin *et al.* 2012). Sampling locations were fixed throughout the nine-year monitoring program.

In our study, data from 4-6 locations from across Missisquoi Bay were averaged. Saint Albans Bay samples were collected at a single location (Figure 2.1). All sampling was conducted between 10 am and 2 pm. At each site, grab samples were collected just below the water surface in duplicate for nutrient concentration and phytoplankton cell

counts. All phytoplankton samples were preserved in 1% Lugol's iodine solution (APHA 1998). Acid-washed Nalgene high-density polyethylene bottles were used for phosphorus samples, while nitrogen samples were collected in 50 mL polypropylene centrifuge tubes. Total nitrogen (TN) and dissolved inorganic nitrogen (DIN) samples were preserved with sulfuric acid to a pH less than 2 and stored at 4° C until analysis. Total phosphorus (TP) samples were frozen until analysis. Soluble reactive phosphorus (SRP) samples were analyzed within 48 hours of collection.

2.4.2. Sample Processing

Whole water phytoplankton samples were examined using Utermöhl settling chambers, following sedimentation for 1-4 days before enumeration (APHA 1998). Samples were counted using an Olympus IX70 or an Olympus IX71 inverted microscope with phase contrast at 400X. All taxa were identified to at least genus following Prescott (1982). Natural units (i.e., colonies for cyanobacteria) and individual cells were enumerated. Counts continued until 100 units of the most abundant taxa had been observed or 100 fields had been evaluated. For the purposes of public health reporting and fulfilling the protocols of the monitoring program, counts of all taxa were recorded as cellular density (cells mL^{-1}). Densities were calculated using a table of colony sizes and average cell count for each size category (see Rogalus and Watzin 2007). Densities of the most abundant taxa (≥ 1% total abundance) were converted to biovolume using median values of linear phytoplankton measurements recorded from Lake Champlain (A. Shambaugh, *unpublished data*) and standard geometric formulae (Hillebrand *et al.* 1999). The phytoplankton data were combined into major taxonomic groups as follows:

cyanobacteria, bacillariophyceae (diatoms), chlorophytes, cryptophytes, non-diatom chrysophytes, and "other" (which included ciliates, pyrrophytes, and dinoflagellates). Because of their relatively low contribution to the entire dataset, cryptophytes, chrysophytes, and other were combined and designated as "CCO."

SRP samples were filtered using acid-cleaned Nalgene PES syringe filters (0.45 μm pore size) and analyzed following the ascorbic acid method (APHA 1998) using a Shimadzu UV-1601 spectrophotometer. TP samples were digested using ammonium persulfate and analyzed following Quickchem™ Method 10-115-01-1-F using a Lachat Quickchem™ 8000 Series Flow Injection Analyzer. Filtered DIN and un-filtered TN samples were analyzed using persulfate digestion (APHA 1998) following Quickchem™ Method 10-107-06-2-H using the Lachat Analyzer.

2.4.3. Statistical Analyses

For the purposes of this study, early season (June and early July) and late season (latter half of October and November) samples were excluded from the dataset to focus on the period of highest sampling frequency. To improve our ability to make comparisons among years and to adjust for any gaps in the data, samples were averaged by two-week time intervals. The intervals, numbered 1 - 6, encompassed the second half of July through the first half of October (see Table 2.2). All phytoplankton abundances were log (x+1) transformed to normalize variation. Analysis of Variance (ANOVA) was used to test for differences among groups were completed using JMP Pro 10.0 (SAS Institute, Inc., Cary, NC).

Redundancy analysis (RDA) was selected to evaluate the relationships among the nutrient variables and phytoplankton community composition from each bay. RDA is a constrained ordination method, which can incorporate many environmental variables and species responses simultaneously (ter Braak 1994, McCune and Grace 2002). RDA was used to search for associations between nutrient concentrations and phytoplankton community composition by bay. We selected all of the nutrient concentration variables (TN, TP, DIN, and SRP) and biovolume of the most abundant phytoplankton genera (Table 2.3) to evaluate associations between nutrient concentrations and phytoplankton. To test if the ordination results were significantly different from those that could have been derived from chance alone, a Monte Carlo permutation test with 999 permutations was conducted on the first ordination axes of each RDA. The RDA analyses were performed using PC-ORD, Version 6.07 (McCune and Mefford 1999).

2.5. Results

2.5.1. Nutrient Trends

The total number of samples for all years of the monitoring program (2003 -2011) was greater for Missisquoi Bay (n = 82) than Saint Albans Bay (n = 43) and varied among the years of the program. In Missisquoi Bay, samples collected per time interval ranged from a minimum of 11 in late September to a maximum of 17 in late August (mean = 14 samples per interval). For Saint Albans Bay, samples collected per time interval ranged from a minimum of 4 in late July to a maximum of 11 in late August (mean = 7 samples per interval).

Mean TP concentration in each bay had a small range, but when all years of data were combined, seasonal patterns were evident (Table 2.2). In both bays, mean concentrations generally increased over the course of the summer (Table 2.2). TP was lower in Saint Albans than Missisquoi Bay over the entire dataset (ANOVA, $p < 0.001$) as well as in every individual interval (Table 2.2). The highest TP single concentrations in each bay were recorded in October (max = 231 μg L^{-1} in Missisquoi Bay; 397 μg L^{-1}; in Saint Albans Bay).

Mean TN concentration in each bay also had a small range, but seasonal patterns were clear and occurred similarly between the two bays (Table 2.2). TN was lower in Saint Albans Bay than in Missisquoi Bay throughout all years of the monitoring program (ANOVA, $p < 0.001$). The highest single TN concentrations recorded occurred in August in both Missisquoi Bay (3.75 mg L^{-1}) and in Saint Albans Bay (2.71 mg L^{-1}). Mean TN was higher in Missisquoi Bay than in Saint Albans Bay for individual intervals 1, 5 and 6.

Mean values of TN:TP were consistently lower in Missisquoi Bay than in Saint Albans Bay over the entire dataset (ANOVA, $p = 0.005$, Table 2.2). There was no difference between the bays in July through early September (intervals 1 - 4), but during September into October (intervals 5 and 6), the TN:TP ratio was lower in Missisquoi Bay. The single highest concentrations of SRP recorded were in September (interval 5) in both Missisquoi Bay (88.7 μg L^{-1}) and Saint Albans Bay (32.2 μg L^{-1}). DIN concentrations peaked in August (interval 2) in both Missisquoi Bay (3.34 mg L^{-1}) and Saint Albans Bay (2.98 mg L^{-1}). Concentrations of DIN were similar in both bays throughout August and early September (intervals 2 - 4) but higher in Missisquoi Bay in

late July, and again in late September and early October. In both bays, concentrations declined from an August peak (Table 2.2). The SRP:DIN ratio was lower in Missisquoi Bay throughout most of the time intervals.

2.5.2. Phytoplankton Community Composition

Over the course of the nine-year monitoring program, 92 algal genera occurred in both bays within six taxonomic groups: 16 cyanobacteria, 15 diatoms, 40 chlorophytes, seven chrysophytes, five cryptophytes, and nine in other groups. Cyanobacteria dominated the community of both bays in every summer, with the exception of 2007 in Missisquoi Bay. Over the entire dataset, the cellular abundance (cells mL^{-1}) of phytoplankton was comprised of greater than 75% cyanobacteria. The mean relative abundance over the entire monitoring program of the most common and potentially toxic cyanobacteria (*Aphanizomenon*, *Anabaena*, and *Microcystis*) was 53% in Missisquoi Bay and 45% in Saint Albans Bay.

The nine most common genera comprised 94.2% of mean annual abundance in the nine-year program (Table 2.3). Of these nine genera, seven were cyanobacteria. The remaining two were relatively large-celled phytoplankton (*Chroomonas* and *Aulocoseira*), so their proportional contribution to community composition is substantially higher when considering biovolume rather than cellular abundance (Table 2.3). In the time intervals when cyanobacteria blooms were most dense, the relative contribution of these taxa was low. For example, in late August (interval 3), the combined mean abundance for *Chroomonas* and *Aulocoseira* was less than 15% in both

bays.

Mean annual phytoplankton abundance was higher in Missisquoi Bay than Saint Albans Bay for the whole dataset ($p = 0.001$). Mean abundance patterns by interval indicated that cyanobacteria blooms in Missisquoi Bay peaked earlier, in late July and early August (intervals 1-2), while the pattern for Saint Albans Bay resembled a more normal distribution, with a peak in late August (interval 3, Figure 2.2). Among cyanobacteria, the relative contribution of genera differed between the bays. *Microcystis* dominated the cyanobacteria community of Missisquoi Bay with a mean percent composition over the entire dataset of 39.6 % and a single maximum per interval of 91.8 % of total phytoplankton abundance in late July (interval 3). The mean abundance of *Microcystis* was higher in Missisquoi Bay than in Saint Albans Bay over the entire dataset ($p < 0.001$). Conversely, *Aphanizomenon* and *Anabaena* dominated the cyanobacteria community of Saint Albans Bay. The mean percent composition for all years of both genera combined was 34.2 % with a single maximum per interval of 89.4 % in early August (interval 5). The mean relative abundance of *Anabaena* was higher in Saint Albans Bay than Missisquoi Bay in late summer (intervals 3, 4, and 5; $p = 0.004$, 0.043, and 0.023, respectively).

Over all years of the monitoring program, trends in the mean relative abundance of each of the non-cyanobacteria phytoplankton taxonomic groups were similar between the bays (Figure 2.3). The relative abundance of chlorophytes and CCO were higher in Saint Albans Bay in late July and early August (intervals 1 and 2). The composition of these groups indicated some differences between the two bays (Figure 2.4 a-c), but few

other consistent patterns. Over the whole dataset, diatom abundance and percent composition were similar in both bays; however, at the end of the summer diatom abundance was higher in Missisquoi Bay (interval 6; $p = 0.043$; Figure 2.4 a). The most common genus of diatom was *Aulocoseira*. Long-tem trends in chlorophyte abundance were not different between bays over most of the monitoring period, but they were marginally more abundant in Saint Albans Bay in early August (interval 2; $p = 0.05$; Figure 2.4 b). The mean abundance of CCO over the whole dataset was higher in Missisquoi Bay ($p = 0.001$ Figure 2.4 c).

There was considerable inter-annual variability in total phytoplankton abundance between and within bays, but the patterns were not consistent. For example, in 2007 there was no cyanobacteria bloom in Missisquoi Bay and overall abundance of phytoplankton was lower than any other year ($p < 0.001$). However, there was no significant reduction in cyanobacteria abundance in Saint Albans Bay in 2007 (Figure 2.5). In fact, that was the only year of the monitoring program for which the annual mean relative abundance of cyanobacteria was higher in Saint Albans Bay (71 %) than in Missisquoi Bay (24 %; $p = 0.003$). In 2008, an unusually dense *Microcystis* bloom occurred in Missisquoi Bay but no substantial increase in algal density compared to other years was observed in Saint Albans Bay (Figure 2.5).

2.5.3. Phytoplankton Community in Relation to Environmental Factors

In the RDA ordinations, major phytoplankton genera are displayed on axes that are constrained to be linear combinations of the nutrient concentration data (Figure 2.6). The nutrient variables each form axes of strongest influence, represented by vectors

radiating from the origin. Each nutrient vector extends towards the genus and site scores to which it is most closely associated (Figure 2.6). We did not identify strong relationships between any of the measured nutrient concentrations and the biovolume of phytoplankton genera for either bay. All together, the nutrient variables explained 5.8% (Missisquoi Bay) and 10.5% (Saint Albans Bay) of the total variance in the phytoplankton data for all years of the monitoring program.

For Missisquoi Bay, RDA Axis 1 represents a small gradient from relatively higher SRP to higher TP (4.6% of total variance) while Axis 2 represents a gradient from higher TP to all other nutrient measurements (1.2%, Figure 2.6a). For Saint Albans Bay, RDA Axis 1 represents a short gradient driven more by total to dissolved nutrients (8.0%) and Axis 2 represents small differences in the importance of P versus N (2.4%, Figure 2.6b).

The projection of each phytoplankton genus on the RDA axes indicates their association with the environmental variables. Site scores (open circles) that are closer together on the graph are more similar in species composition and association with the nutrient variables (ter Braak 1994). For Missisquoi Bay, sites were not strongly separated by whether they had more *Anabaena* or more *Aulocoseira*, especially relative to genus scores clustered close to the origin. For Saint Albans Bay, the abundance of *Aulocoseira* strongly separated sites scores, especially relative to *Coelosphaerium* and *Aphanocapsa*. For both bays, randomization tests indicated that the interaction between phytoplankton biovolume and the nutrient variables for the first RDA axes were not likely due to chance alone (Missisquoi Bay: $p = 0.049$, Saint Albans Bay: $p = 0.043$), however, the amount of

variation captured was very small.

2.6. Discussion

In this study, nutrient concentrations did not have high explanatory power with regards to phytoplankton community composition. High nutrient concentrations are a pre-requisite for dense algal growth but the composition, timing, and predictability of blooms are difficult to forecast based on nutrient data alone (Hyenstrand *et al.* 1998, Scheffer *et al.* 2003, Roelke *et al.* 2007). The analysis of the monitoring program dataset for Missisquoi Bay and Saint Albans Bay, Lake Champlain provided a characterization of the summer nutrient concentrations and phytoplankton community composition from 2003-2011. We suggest some areas where future research on shallow eutrophic lakes might be focused.

Long-term trends in phytoplankton community composition can be chaotic and unpredictable because of complexities among several independently varying factors and high niche-overlap among taxa (Downing *et al.* 2001, Scheffer *et al.* 2003). Studies show distinct seasonal patterns of phytoplankton assemblages but also considerable inter-annual variation within individual lakes (Anneville *et al.* 2002, Roelke *et al.* 2007, Suikkanen *et al.* 2007, Lefebvre *et al.* 2011). In Missisquoi and Saint Albans Bays, it is likely that interactions among several factors led to the observed inter-annual variability and differences in the phytoplankton assemblages.

The overall concentrations of N and P were higher throughout the monitoring program in Missisquoi Bay than in Saint Albans Bay (Table 2.2). Despite close proximity

and the fact that both Missisquoi Bay and Saint Albans Bay are dominated by cyanobacteria in late summer, the phytoplankton communities differed in taxonomic composition on a seasonal and inter-annual basis. Cyanobacteria blooms in Missisquoi Bay began earlier in the summer and had higher mean cellular abundance than in Saint Albans Bay (Figure 2.2). RDA indicated that phytoplankton community composition was not strongly related to the measured nutrient variables in either bay during peak bloom conditions. These findings are in agreement with other recent studies in Missisquoi Bay that suggest that water column nutrient concentrations alone cannot explain phytoplankton dynamics, especially once a dense cyanobacteria bloom is underway (Smith *et al.* 2011, Hart *et al.* 2013, Pearce *et al.* 2013). Nutrients may play a larger role in determining species composition prior to the development of the blooms.

Alternate strategies for nutrient uptake among types of cyanobacteria and differences between the two bays in physical structure are factors that can help to explain the observed differences in composition among the cyanobacteria taxa (Dokulil and Teubner 2000, Scheffer *et al.* 2003). Compared to Saint Albans Bay, Missisquoi Bay is uniformly shallow, more evenly mixed vertically (Figure 2.1, Table 2.1). The cyanobacteria of Missisquoi Bay was comprised of a higher proportion of *Microcystis*. The capability of *Microcystis* to regulate cellular buoyancy can give it an advantage over other algal species in shallow lakes where internal loading of N and P occurs and hydrodynamic stability is high (Bormans *et al.* 1999, Dokulil and Teubner 2000). In Missisquoi Bay, internal loading of N and P is highest during periods of sediment anoxia in late summer and fall (Smith, et al. 2011, Pearce et al. 2013). Vertical migration by

colonies of *Microcystis* to this pool of available nutrients at the sediment surface is an advantageous strategy to cope with rapid fluctuations in nutrient availability at the water surface (Reynolds 1998, Scheffer and van Nes 2007).

Compared to Missisquoi Bay, Saint Albans Bay had lower concentrations of both N and P, and a lower N:P ratio in late summer and fall (Table 2.2). Cyanobacteria blooms in Saint Albans Bay were of shorter duration, lower density and dominated more by *Anabaena* than Missisquoi Bay (Table 2.2). Because *Anabaena* is capable of fixing atmospheric nitrogen and is not solely dependent on nutrients available in the water column (Dokulil and Teubner 2000), lower TN and DIN concentrations in Saint Albans Bay might help explain why *Anabaena* was more dominant in that system. *Anabaena* has been one of the dominant genera of the phytoplankton community in Saint Albans Bay for over 40 years, though annual bloom densities have increased in recent decades (Smeltzer *et al.* 2012). Regardless of the high total concentrations of nutrients, daily N-depletion can occur in eutrophic systems, such as both of our study sites and this favors N-fixing or vertically migrating cyanobacteria (Hyenstrand *et al.* 1998, Downing *et al.* 2001).

In Missisquoi Bay and Saint Albans Bays, interactions between cyanobacteria and diatoms and zooplankton grazers may be important in determining phytoplankton community composition since nutrient concentrations alone were not sufficient for explaining long-term trends in phytoplankton community composition in either bay (Figure 2.6). In several areas of Lake Champlain, spring diatom blooms are widespread (Levine *et al.* 2012, Smeltzer *et al.* 2012). During early summer, a depletion of silica and

consequently diatom bloom collapse can enhance conditions that favor dominance by cyanobacteria by reducing competition for both N and P (Schindler 2006, Lefebvre *et al.* 2011). The diatom *Aulocoseira* had a stronger effect in separating site scores than other variables in the RDA, particularly for Saint Albans Bay (Figure 2.6). This genus contributes substantially to the biovolume of phytoplankton in both bays (Table 2.3) so the interplay between diatoms and cyanobacteria during bloom initiation in shallow bays of Lake Champlain warrants further investigation.

In many eutrophic lakes, trophic dynamics and invasive species play an important role in determining phytoplankton community composition (Brett and Goldman 1997, Carpenter *et al.* 2001, Schindler 2006, Hambright *et al.* 2007). In Missisquoi Bay, both white perch (*Morone americana*) and alewife (*Alosa pseudoharengus*) have been observed to feed selectively on large zooplankton in June and July (R. Gorney, *unpublished data*). Planktivory by alewife has been associated with a decline in the biomass of large zooplankton in several shallow bays of Lake Champlain (Mihuc *et al.* 2012). A release of grazing-induced mortality on phytoplankton increases the likelihood that large colonies of grazing-resistant or competitively superior phytoplankton, such as cyanobacteria, will dominate the community (Brooks and Dodson 1965, Elser 1999, Downing *et al.* 2001, Hambright *et al.* 2007). Invasive planktivorous fish can lead to long-term shifts in phytoplankton community through predation on the zooplankton grazer community (Roelke *et al.* 2007, Suikkanen *et al.* 2007), so measuring their impacts on trophic structure is an important research need in Lake Champlain.

This monitoring program was designed to serve a public health and notification

purpose and did not perfectly fit the purpose of identifying environmental triggers of cyanobacteria blooms in these shallow bays. Several physical and biological parameters that were not regularly measured, such as water temperature, light, and zooplankton abundance could help explain seasonal patterns in phytoplankton composition (Hyenstrand *et al.* 1998, Reynolds 1998, Elser 1999, Hambright *et al.* 2007). Adaptive management and adjustments to monitoring protocols will improve our ability to fulfill public health priorities and better understand ecological processes (Nichols and Williams 2006, Lindenmayer and Likens 2010).

The results of this study are useful for informing research, management, and the design of future monitoring programs in shallow eutrophic systems. Missisquoi Bay and Saint Albans Bay possess dynamic phytoplankton assemblages and a small number of cyanobacteria genera dominate both bays each summer. Our evaluation of seasonal and inter-annual trends in community composition illuminated several differences between the bays and among years. We attempted to explain these patterns using nutrient concentrations, but found that large amounts of variation remained unexplained. Future research and monitoring programs in shallow eutrophic systems prone to cyanobacteria blooms should include detailed measurements of light availability, water column stability, and trophic structure to better understand or predict cyanobacteria bloom dynamics.

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2.8. References

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Table 2.1: Morphometric and chemical characteristics of Missisquoi and Saint Albans Bays, Lake Champlain (Troy *et al.* 2007).

	Missisquoi Bay	Saint Albans Bay
Mean depth (m)	3	8
Max depth (m)	4	12
Water surface area (km^2)	78	7
Watershed area (km^2)	3105	130
Annual P load ($kg\ km^{-2}\ y^{-1}$)	1931	940
Land use:		
Forest %	67	28
Agriculture %	25	53
Urban %	7	16

Table 2.2: Mean nutrient concentrations and TN:TP ratio (± SE) over the entire monitoring program (2003-2011) for Missisquoi Bay (MB) and Saint Albans Bay (SA). TP: total phosphorus; TN: total nitrogen; SRP: soluble reactive phosphorus; DIN: dissolved inorganic nitrogen. Asterisks (*) indicate the greater value (ANOVA, $p < 0.05$) when there was a significant difference between the bays within the same interval or in mean of the entire dataset.

	Time Interval	TN (mg/L)		TP (µg/L)		TN:TP	
		MB	SA	MB	SA	MB	SA
Late July	1	0.80 ± 0.05*	0.50 ± 0.04	44.69 ± 1.77*	29.79 ± 1.63	18.09 ± 1.07	17.35 ± 1.88
Early Aug.	2	0.89 ± 0.18	0.68 ± 0.19	67.11 ± 8.88*	37.56 ± 4.43	13.38 ± 1.76	19.30 ± 5.77
Late Aug.	3	0.92 ± 0.18	0.79 ± 0.16	70.31 ± 5.15*	42.85 ± 4.50	12.51 ± 1.63	19.75 ± 4.15
Early Sept.	4	0.92 ± 0.18	0.63 ± 0.14	79.52 ± 5.95*	38.47 ± 2.57	11.41 ± 1.68	19.34 ± 6.42
Late Sept.	5	0.73 ± 0.08*	0.47 ± 0.04	68.24 ± 5.10*	32.57 ± 2.07	10.81 ± 0.69	14.47 ± 0.74*
Early Oct.	6	0.75 ± 0.09*	0.40 ± 0.02	77.64 ± 11.93*	29.25 ± 2.80	10.48 ± 0.65	14.97 ± 1.14*
Mean		0.82 ± 0.04*	0.59 ± 0.04	65.76 ± 2.75*	36.47 ± 2.83	13.35 ± 1.29	18.62 ± 1.34*
		DIN (mg/L)		SRP (µg/L)		DIN:SRP	
		MB	SA	MB	SA	MB	SA
Late July	1	0.62 ± 0.05*	0.39 ± 0.03	3.65 ± 0.59	3.08 ± 0.71	292.74 ± 52.83	409.10 ± 170.54
Early Aug.	2	0.69 ± 0.19	0.54 ± 0.17	7.45 ± 1.59*	2.94 ± 0.65	135.03 ± 25.92	331.57 ± 88.36*
Late Aug.	3	0.67 ± 0.19	0.58 ± 0.16	7.02 ± 1.10*	2.12 ± 0.79	100.65 ± 24.55	836.41 ± 396.64
Early Sept.	4	0.64 ± 0.16	0.57 ± 0.16	9.28 ± 1.58*	3.54 ± 0.69	103.67 ± 29.45	270.70 ± 73.39*
Late Sept.	5	0.49 ± 0.04*	0.39 ± 0.02	13.36 ± 5.60	3.99 ± 2.05	72.69 ± 14.29	256.58 ± 64.45*
Early Oct.	6	0.51 ± 0.04*	0.34 ± 0.02	13.63 ± 5.54	4.26 ± 1.71	65.57 ± 10.13	159.53 ± 38.15*
Mean		0.63 ± 0.04*	0.46 ± 0.04	8.75 ± 0.79*	4.00 ± 0.81	132.2 ± 15.1	378.9 ± 76.17*

Table 2.3: Summary data of the most common genera of phytoplankton (≥1% total abundance) in Missisquoi Bay and Saint Albans Bay, Lake Champlain. Abundance (cells mL^{-1}), biovolume (10,000 μm3 mL^{-1}) and "%" (percent composition) were averaged over the entire monitoring program (2003-2011).

			Missisquoi Bay				Saint Albans Bay			
			Abundance		Biovolume		Abundance		Biovolume	
Group	Genus	RDA Name	Mean	%	Mean	%	Mean	%	Mean	%
Cyanobacteria	*Microcystis*	MICRO	26,162	39.6	1,712	26.7	4,298	15.7	281	8.9
Cyanobacteria	*Chroococcus*	CHROC	9,268	18.4	728	13.7	3,253	14.7	255	9.9
Cyanobacteria	*Anabaena*	ANABA	8,493	14.4	1,019	15.6	11,675	29.0	1,401	29.5
Cyanobacteria	*Aphanizomenon*	APHAN	4,962	7.3	564	6.6	1,480	5.3	168	5.3
Cyanobacteria	*Aphanocapsa*	CAPSA	1,331	2.0	14	0.2	920	3.9	10	0.4
Cyanobacteria	*Aphanothece*	THESE	1,276	1.4	3	0.0	613	1.5	2	0.0
Cyanobacteria	*Coelosphaerium*	COELO	270	0.4	8	0.1	2,995	7.0	90	2.1
Cryptophyte	*Chroomonas*	CHROM	684	2.9	684	18.7	504	4.4	504	25.6
Diatom	*Aulocoseira*	AULOC	922	2.5	1,135	18.3	525	2.8	646	18.3
Total			53,368		5,868		26,264		3,357	

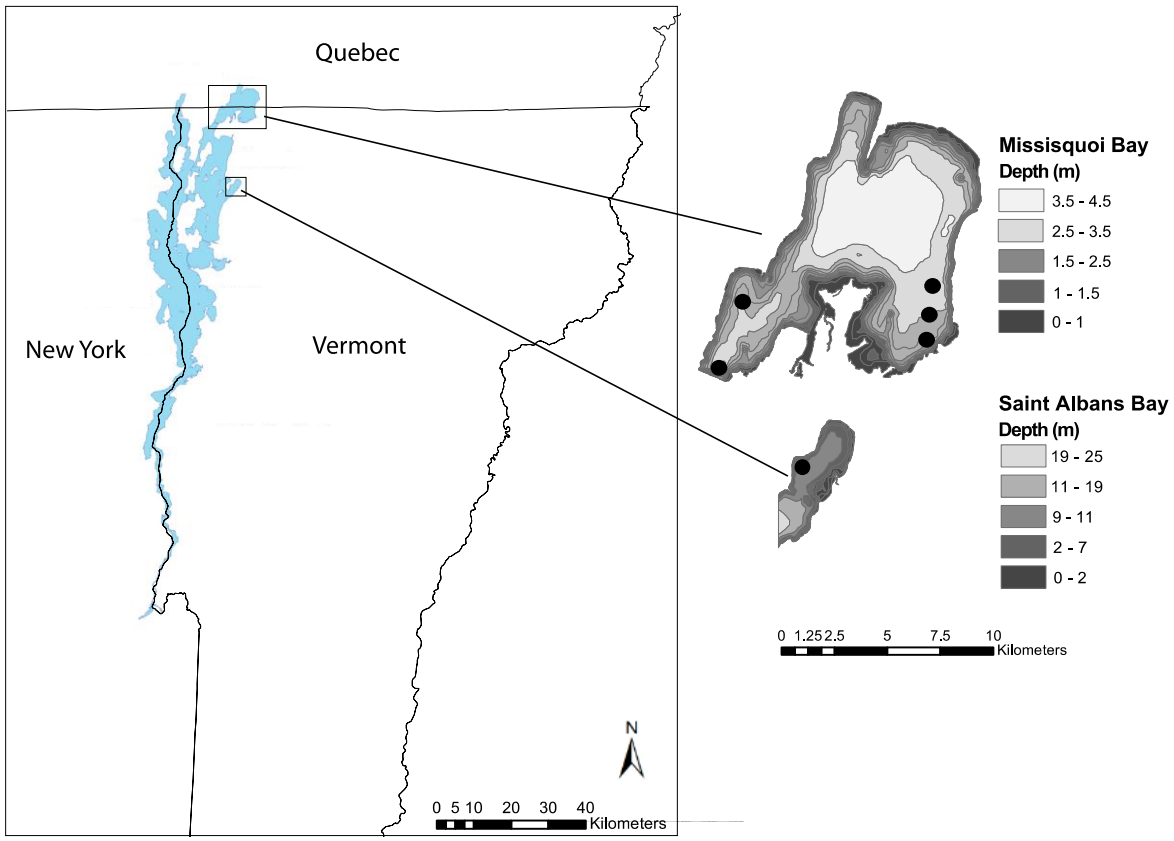

Figure 2.1: Location of Lake Champlain and surrounding region with detailed bathymetric maps of Missisquoi and Saint Albans Bays. Filled circles indicate long-term monitoring sampling locations within each bay.

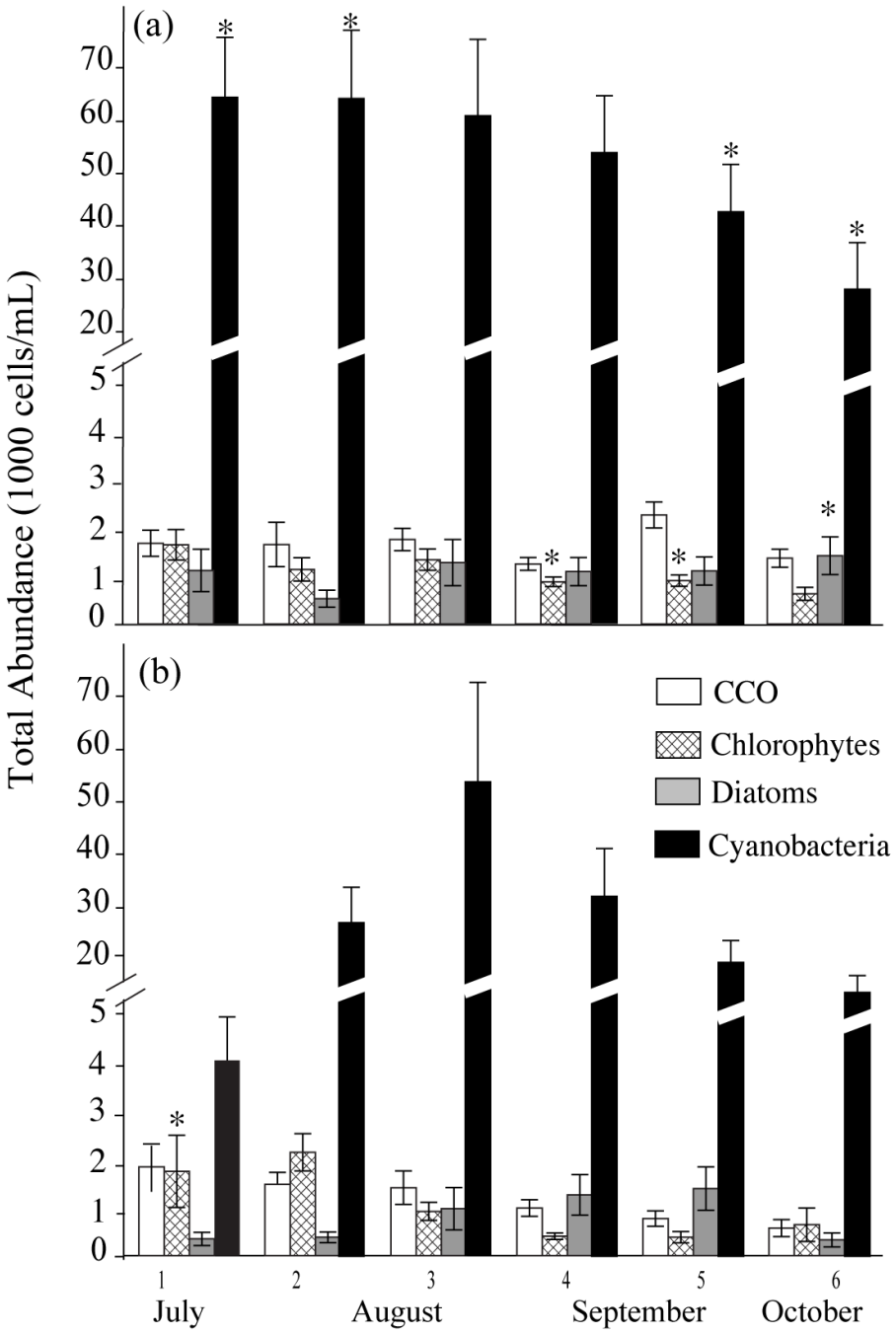

Figure 2.2: Mean total phytoplankton abundance (± SE) by major taxonomic group per time interval over the monitoring program (2003-2011) in (a) Missisquoi Bay and (b) Saint Albans Bay, Lake Champlain. Because of their relatively low abundances, the groups Cryptophytes, Chrysophytes and Other were combined (CCO). Asterisks (*) indicate the greater value if there was a significant difference between the two bays (ANOVA, $p < 0.05$ in all cases).

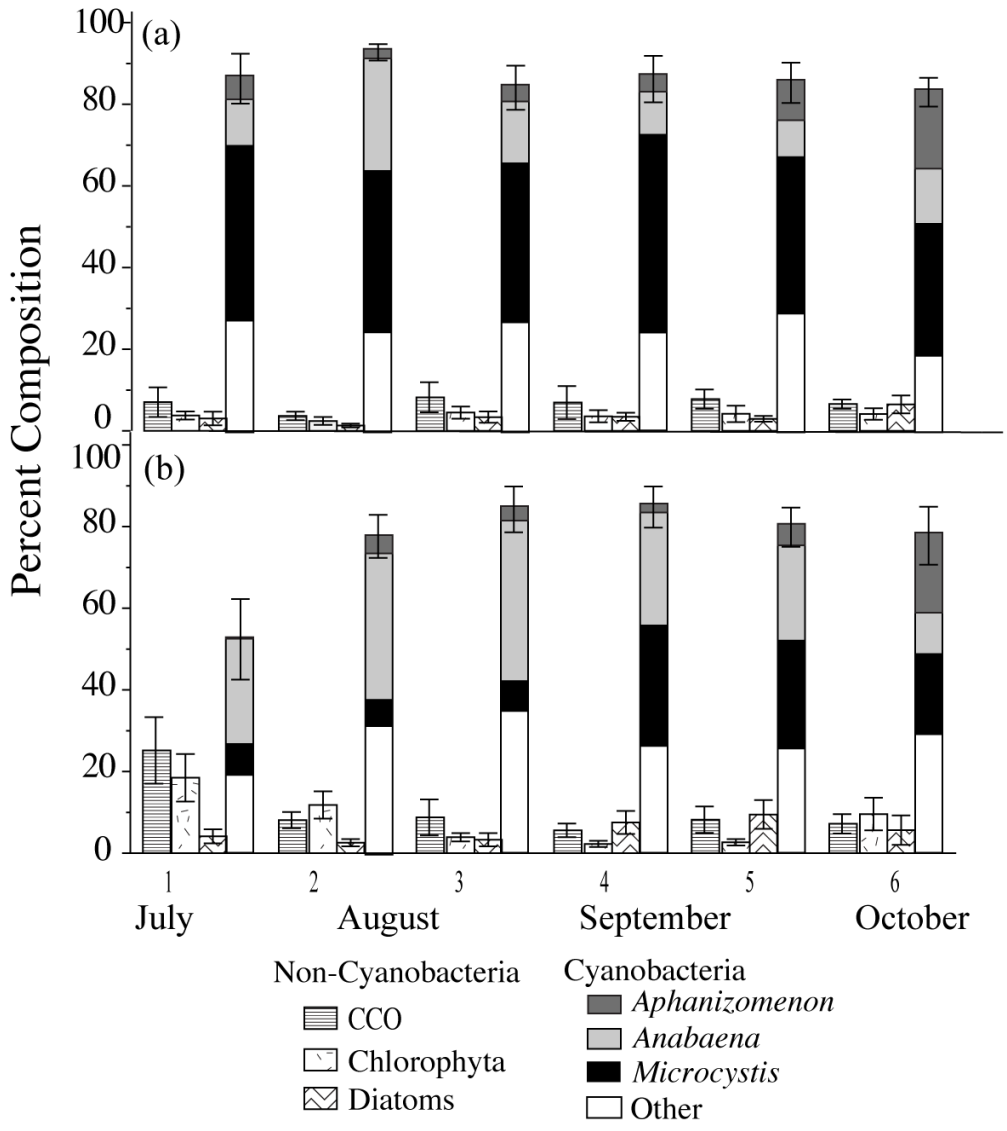

Figure 2.3: Mean percent composition (± SE) of the major phytoplankton taxonomic groups per time interval for the entire monitoring program (2003-2011) in (a) Missisquoi Bay and (b) Saint Albans Bay, Lake Champlain.

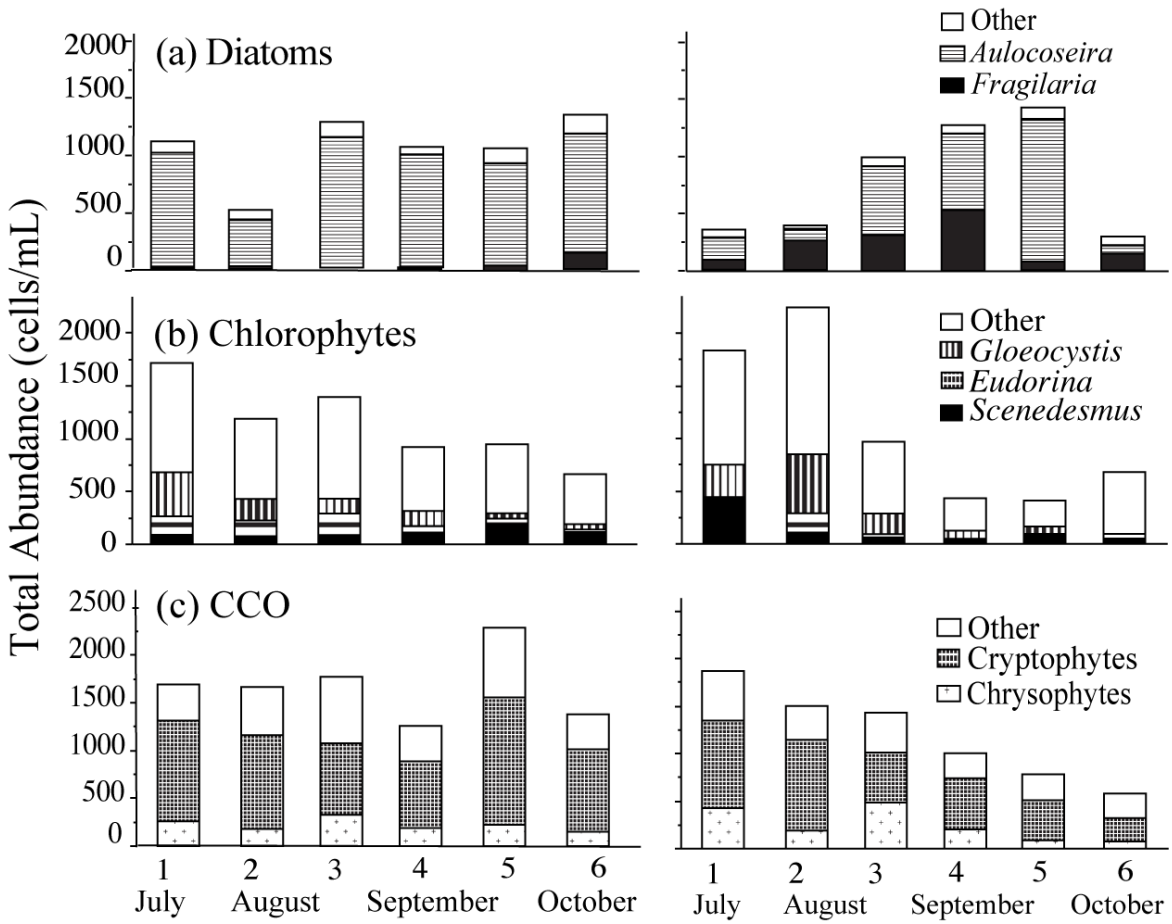

Figure 2.4: Mean seasonal abundance per time interval over the monitoring program (2003-2011) of: (a) Diatoms; (b) Chlorophytes; (c) Cryptophytes, Chrysophytes, and Other (CCO) in Missisquoi Bay (left column) and Saint Albans Bay (right column), Lake Champlain.

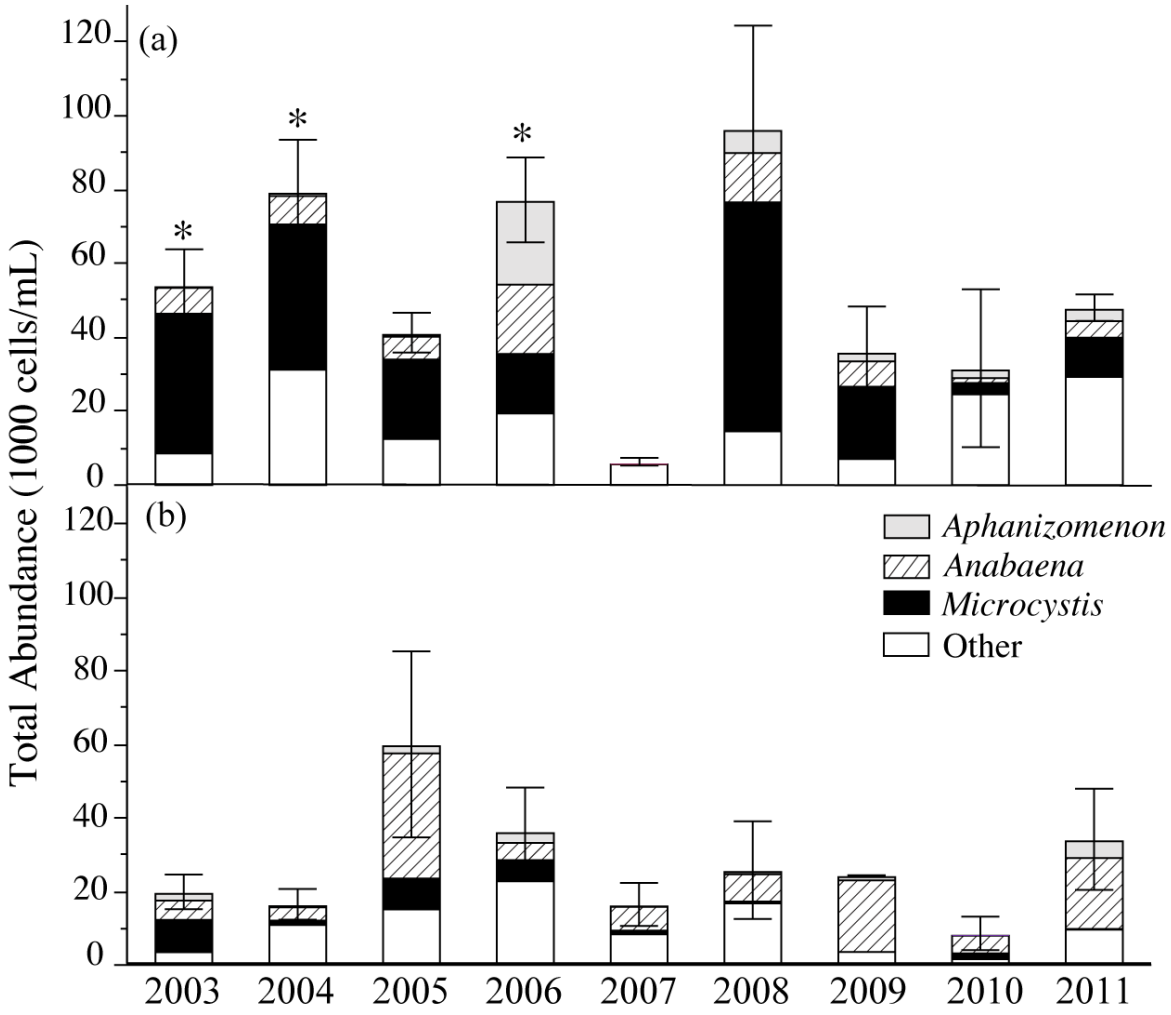

Figure 2.5: Annual means of total abundance (± SE) of major toxin-producing cyanobacteria taxa and all other phytoplankton for 2003-20011 in (a) Missisquoi Bay and (b) Saint Albans Bay, Lake Champlain. Asterisks (*) indicate years where mean total annual abundance was higher in Missisquoi Bay (ANOVA, $p < 0.05$).

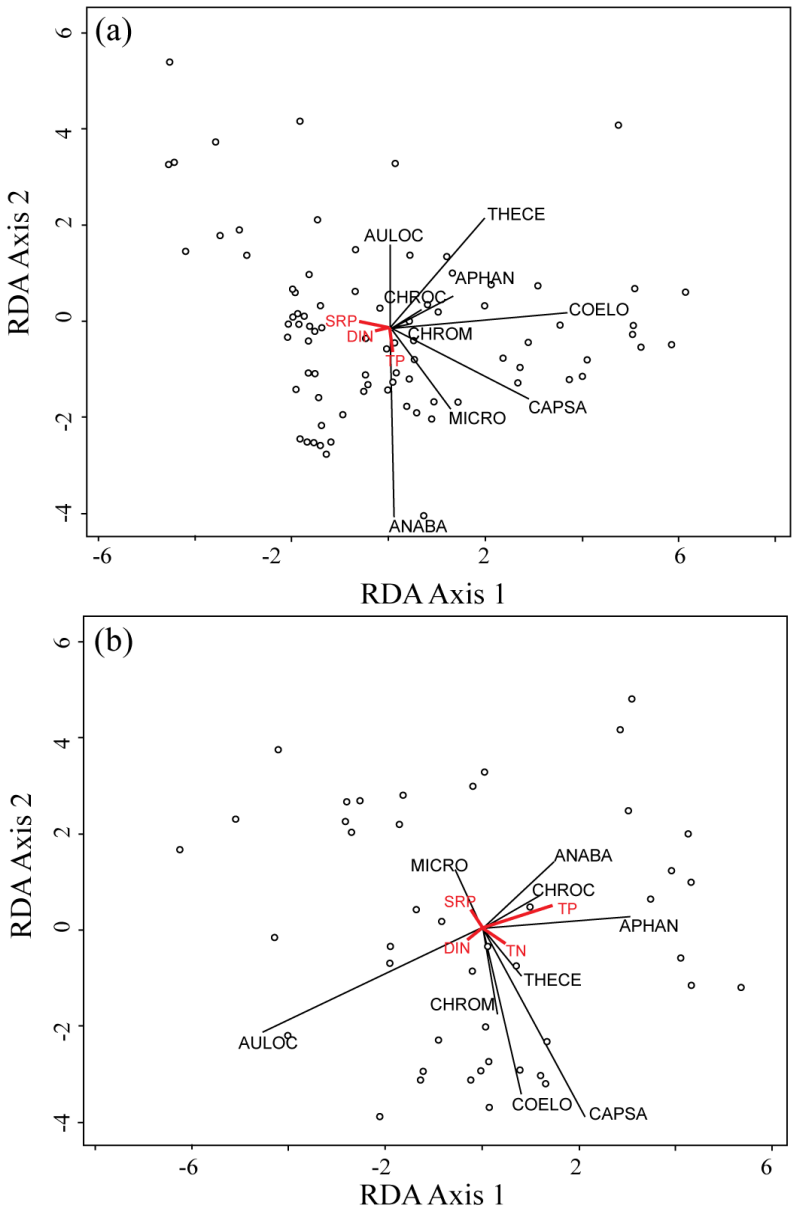

Figure 2.6: Redundancy analysis (RDA) ordination plots of common phytoplankton genera (black vectors) and nutrient concentrations (red vectors) for (a) Missisquoi Bay and (b) Saint Albans Bay. See Table 2.1 for phytoplankton genera codes. Open circles represent individual sample scores in ordination space.

CHAPTER 3: DIET COMPOSITION OF INVASIVE WHITE PERCH (*MORONE AMERICANA*) AND ALEWIFE (*ALOSA PSEUDOHARENGUS*) IN MISSISQUOI BAY, LAKE CHAMPLAIN AND IMPLICATIONS FOR THE ZOOPLANKTON COMMUNITY

3.1. Abstract

Increases in zooplanktivory as a result of the establishment of invasive fish can lead to rapid changes in trophic structure in large lakes. Two non-native planktivorous species, alewife (*Alosa psuedoharengus*) and white perch (*Morone americana*), have recently invaded Lake Champlain. We compared the diet composition of these species in Missisquoi Bay, a shallow and eutrophic bay. The objectives were to (1) characterize the diet composition of adult white perch and adult alewife in 2010 and 2011, (2) describe changes in the ambient zooplankton community using composition data from 1976, 2005, and the current study, and (3) evaluate the ecological impacts of coexistence of both fish species, particularly their selectivity among zooplankton from the ambient community. In addition, white perch diet composition in 2010 and 2011 was compared to data from a 2005 study, prior to invasion by alewife. Fish diet composition and ambient zooplankton were sampled between two and four times per month from April to September. In both years, white perch were omnivorous with periods of substantial zooplanktivory that coincided with periods of *Daphnia* availability, whereas alewife diet was predominantly comprised of zooplankton. Large zooplankton biomass in the bay has declined since 2005 (t-test, $p = 0.04$). When compared to historical data from

1976, declines in large zooplankton are even more substantial. The Manly-Chesson Selectivity Index suggested that compared to alewife, white perch were more selectively consuming large zooplankton. Changes in the zooplankton community caused by the grazing effects of white perch and alewife planktivory have implications for the trophic dynamics of Missisquoi Bay, Lake Champlain.

3.2. Keywords

Lake Champlain, white perch, alewife, zooplankton, selectivity analysis, diet composition

3.3. Introduction

Fish invasions can have sizeable impacts on lower trophic levels in lake ecosystems, particularly if the invaders are planktivores (Lazzaro 1987, Vanni *et al.* 1997). In what is considered an archetypical example of a trophic cascade, selective predation on large zooplankton by planktivorous fish leads to a depletion of large taxa and an increase in algal biomass (Carpenter *et al.* 1985). This ecosystem-level change can occur rapidly at the front edge of an invasion in systems with previously unexploited prey bases (Wells 1970, Palkovacs *et al.* 2008, Wang *et al.* 2010). In combination with high nutrient concentrations, low nitrogen to phosphorus ratio (N:P), and increased turbidity, the removal of large cladocerans can be a crucial final step in the pathway towards dominance by potentially toxic cyanobacteria blooms (Elser 1999).

Two planktivorous fish species, alewife (*Alosa pseudoharengus*) and white perch (*Morone americana*), have successfully invaded all of the Laurentian Great Lakes (Christie 1974, Madenjian *et al.* 2008). Both species have invaded Lake Champlain much more recently than the Great Lakes and the full extent of their impacts on the Lake

Champlain food web remain to be seen (Marsden and Hauser 2009). Invasion by white perch began in 1984 and they are now common lake-wide (Hawes and Parrish 2003). Alewife were first observed in Lake Champlain in 2003 and by 2007 they were also found throughout the lake (Marsden and Hauser 2009).

Both species are capable of rapid population expansions when introduced into new favorable habitats and can have substantial overlap in their diet composition, both as juveniles (Prout *et al.* 1990, Gopalan *et al.* 1998), and as adults (Hurley 1992, Moring and Mink 2002, Post *et al.* 2008). White perch and alewife are native to the same region of the coastal Atlantic Ocean, and they can be competitors for some prey resources, particularly large zooplankton such as *Daphnia* (Hurley 1992, Moring and Mink 2002). For both species to thrive, resource partitioning is likely to occur (Schoener 1974, Chesson 2000). Though they co-exist in many water bodies, few studies have focused specifically on the interactions of these two species as concurrent recent invasive species.

White perch are effective invaders because they are an opportunistic species and they tend to feed low on the food chain despite their size (Weis 2005, Kerr and Secor 2012). Their diet composition is highly variable among water bodies and habitat types and both adults and juvenile fish can consume large quantities of zooplankton (Gopalan *et al.* 1998, Guzzo *et al.* 2013). High growth rates and diet plasticity have enabled white perch to outcompete native fish species for food resources in many systems that they have invaded (Parrish and Margraf 1990, Prout *et al.* 1990, Feiner *et al.* 2013, Guzzo *et al.* 2013).

Invasions by alewife have had widespread and long-lasting impacts on the food webs of the Great Lakes and other lakes. The potential impacts of alewife include shifts in zooplankton community structure, native fish declines through multiple mechanisms, and increases in phytoplankton abundance (Harman *et al.* 2002, Madenjian *et al.* 2008, Wang *et al.* 2010). The presence of invasive planktivorous fish such as alewife and white perch is one of the many factors that have led to changes in the food webs of the Great Lakes, particularly in Lakes Ontario, Huron, and Michigan (Mills *et al.* 2003, Madenjian *et al.* 2008).

In this study we investigated the diet composition of adult alewife and white perch along with temporal trends in the zooplankton community composition in Missisquoi Bay, a shallow, eutrophic bay in northern Lake Champlain. Data collected in 1976-1977 indicated that the zooplankton community was dominated by large cladocerans and the system was not highly productive at that time (Keen and Potash 1978). In the last few decades, the bay has become eutrophic as a result of increases in nutrient loading and sedimentation (Levine *et al.* 2012, Smeltzer *et al.* 2012).

A study conducted in 2005 (Couture and Watzin 2008), prior to alewife invasion in Missisquoi Bay, showed evidence of zooplanktivory by adult white perch (140 - 301 mm total length) in early summer. White perch are opportunistically zooplanktivorous and often select for the largest zooplankton taxa, but they additionally will consume fish eggs, benthos, and small fish (Moring and Mink 2002, Guzzo *et al.* 2013). We hypothesized that overlap in diet composition between white perch and alewife could lead to a decline in the biomass of large zooplankton in Missisquoi Bay. We also

expected an increase in the relative biomass of smaller zooplankton such as *Bosmina* as large zooplankton populations declined. Our specific objectives were to (1) characterize the diet composition of adult white perch and adult alewife in 2010 and 2011, (2) describe changes in the ambient zooplankton community using historical and current composition data, and (3) compare the selectivity of both fish species in their consumption of zooplankton from the ambient community to determine the potential for direct diet overlap between the species.

3.4. Methods

Lake Champlain is a long, narrow lake with a maximum width of 20 km and a length of 193 km. Missisquoi Bay is a eutrophic and shallow bay (maximum depth 5 m, surface area approximately 77.5 km^2) at the northern end of the lake with 58% of its watershed in Vermont and the remainder in the province of Quebec, Canada. The bay has undergone substantial ecological change in recent decades as nutrient concentrations have increased and dense annual cyanobacteria blooms are common (Levine *et al.* 2012, Smeltzer *et al.* 2012).

We collected fish and zooplankton weekly or once every two weeks from April to September in both 2010 and 2011 from the same locations and using the same methods as a previous diet study in Missisquoi Bay (Couture and Watzin 2008). Two or three 30.5 m by 1.5 m gillnets, each with four panels of mesh size ranging from 12.7 to 57.2 mm bar mesh in 6.5 mm increments were set in 2-3 m water depth for two hours to minimize digestion time. The timing of the sampling varied over the course of study (from dawn to

just after dusk) following a determination that stomach fullness of both species was not strongly linked to time of day (R. Gorney, *unpublished data*). In April and May 2010, alewife and white perch were sampled using a 180 m x 1.8 m beach seine as part of a long-term monitoring program by the Vermont Department of Fish and Wildlife. On each collection date, up to 30 white perch and 30 alewife were retained for laboratory diet analysis. Fish were immediately frozen in the field using dry ice to halt digestion.

All of the fish collected for diet analysis were measured for total length (TL, mm) and weight (g) before removal of contents in the gastrointestinal tract anterior to the pyloric caecum. Contents of stomachs that contained large quantities of zooplankton were sub-sampled using a 5 ml Henson-Stemple pipette in a water suspension until 200 organisms (± 20%) were counted. The volume of the subsample was typically 5-20% of the total sample and the total number of organisms in the stomach was estimated from the subsample by direct proportion. Stomach contents were separated and quantified. Prey items were sorted into four major classification groups: fish, benthos, zooplankton and other organisms. Zooplankton were identified to the following taxonomic groups: calanoid copepods, cyclopoid copepods, *Daphnia* spp., small cladocerans, and large cladocerans (see Table 3.1 for complete species list). Prey items were separated and dry weights of each major group were obtained by drying items at 80°C for at least 24 hours. Diet composition was expressed as mean monthly percent composition by abundance and by dry weight of each taxon. Proportions were estimated for each individual fish and then averaged across fish for all dates within a month for each year of the study.

On each date that fish were sampled, ambient zooplankton were collected using a vertical tow through the entire water column using a 63-µm mesh, 15-cm diameter Wisconsin-style plankton net. Samples were preserved in 70% ethanol (APHA 1998). Mean monthly zooplankton density (individuals L^{-1}) was calculated from duplicate samples collected on each collection date within each month. Length measurements were collected for a subset of zooplankton in both 2010 and 2011. Species-specific length-mass regressions were applied to estimate zooplankton biomass (Downing and Rigler 1984). Neither the 2005 data nor the historical zooplankton data collected monthly in 1976 -77 included information on length measurements. We applied current species length measurements to estimate zooplankton biomass, with the acknowledgement that this provides only an estimate of the historical biomass.

Prey selectivity of each fish was calculated using the Manly-Chesson Selectivity Index, which is based on a comparison of the relative abundance of a prey item in the environment with the abundance in the diet (Chesson 1983):

$$\alpha_i = (r_i / n_i) / \sum_{i=1}^{m} m r_i / n_i$$

where m is the number of prey species in the diet, r_i is the proportion of ith species ingested, and n_i is the proportion of prey i in the environment. For m prey species in a sample, a value $\geq 1/m$ indicates positive selection of prey species i. In this study, five zooplankton taxonomic categories were used, so positive selection is indicated by any selectivity value $\geq$ 0.2. Only fish with diets that were majority zooplankton ($\geq$ 50%

abundance) were included in calculations of mean monthly selectivity values. For any month with less than three fish fitting that criterion, all were excluded from analysis.

3.5. Results

3.5.1. Fish Abundance and Diet Composition

In 2005, white perch constituted 70% of the total fish catch and alewife were not collected in the study (Couture and Watzin 2008). In 2010, white perch comprised 49% (n = 1,016) and alewife 16% (n = 331) of the total catch (n = 2055). Among 16 sampling days, the catch per unit effort (CPUE) was 9.8 white perch and 4.5 alewife per net-hour^{-1}. Of the white perch and alewife that were retained for diet analysis, 64% (n = 298) of the white perch and 50% (n = 90) of alewife had identifiable stomach contents. In 2011, white perch comprised 62% (n = 753) and alewife 1% (n = 18) of the total catch (n = 1217). Among 12 sampling days, the CPUE was 7.2 white perch and 0.2 alewife per net hour^{-1}. Of the white perch and alewife that were brought back to the lab for analysis, 76% (n = 277) of the white perch and 66% (n = 12) of alewife had identifiable stomach contents (Table 3.2). The white perch collected in 2010 (85-340 mm TL) and 2011 (99-343 mm TL) included fish ranging from young-of-year (YOY) to adult. Similarly, alewife collected in 2010 (69-287 mm TL) and 2011 (91-234 mm TL) also included fish representing several age classes. Other fish commonly captured in our gillnets included yellow perch (*Perca flavescens*), northern pike (*Esox lucius*), and pumpkinseed sunfish (*Lepomis gibbosus*).

The results of the diet analysis indicated that in both 2010 and 2011, white perch were highly omnivorous and diets were highly variable among individual fish. In both years, white perch diets included zooplankton but the consumption of zooplankton was primarily limited to June and July (Figure 3.1), when large zooplankton were most abundant. Consumption of zooplankton by white perch was not related to the size of the fish, as we observed fish of all sizes consuming zooplankton. Benthic invertebrates (particularly burrowing mayflies) were a predominant component of white perch diet in April and May, while YOY and larval fish comprised an increasing proportion of the diet throughout the late summer months in both 2010 and 2011 (Figure 3.1).

Alewife had a considerably narrower diet composition than white perch, primarily comprised of zooplankton in both 2010 (94% mean total abundance) and 2011 (99%). Throughout 2010, alewife diet consisted mostly of calanoid and cyclopoid copepods. In June 2010, *Daphnia* comprised 42% of the diet by abundance but in all other months, diets were at least 60% calanoid and cyclopoid copepods by abundance. Large cladocerans such as *Leptodora* never comprised more than 2% in any month. In 2011, however, alewife diets were quite different, though analysis was based on a small sample size. We only caught alewife in any abundance on one collection date (8 June). The 11 fish collected on that day with identifiable stomach contents had consumed on average 79% *Daphnia* and 12% *Leptodora*, by abundance. A small number of alewife in both years consumed chironomid larvae, fish eggs and YOY fish, often in addition to zooplankton (Table 3.2).

3.5.2. Current and Historical Zooplankton Community Structure

The zooplankton assemblage in 2005 and the two years of this study showed similar trends in dominant taxa by month (Figure 3.2). In late spring, cyclopoid copepods were most abundant, and in early June of each summer, *Daphnia* increased in abundance to become the dominant genus by both abundance and biomass for a short period. In 2005 and 2010, the periods of highest *Daphnia* abundance were similar in duration and timing (mid June to early July). In 2011, this period was longer (extending into late July) and *Daphnia* comprised a greater proportion of the total community biomass but overall zooplankton abundance was still substantially lower than in 2005. Throughout each summer, small cladocerans (mostly *Bosmina*) and cyclopoid copepods increased in abundance and by September of 2010 and 2011, greater than 90% of the community was comprised of these small taxa (Figure 3.2).

The mean proportion of summer zooplankton biomass in Missisquoi Bay comprised of small cladocerans and cyclopoid copepods has increased from 3% in 1976-77, to 56% in 2005, and 71% in the current study (Keen and Potash 1978, Couture and Watzin 2008). Mean summer biomass of all zooplankton decreased from 2005 to 2010 and 2011 (Figure 3.3). Mean summer biomass of large zooplankton (*Daphnia*, large cladocerans, and calanoid copepods) was 60% lower in 2010 and 2011 compared to 2005. In 1976-77, *Daphnia* and *Leptodora* comprised close to 99% of total zooplankton biomass in August and 75% in September (Keen and Potash 1978), compared to 14% and 8% for those months in 2011. Our data suggest that *Leptodora* are now rare in Missisquoi Bay, while in August 1976, that genus comprised approximately 50% of the total

zooplankton biomass in the bay (Keen and Potash 1978). In the current study, the biomass of calanoid copepods in September 2011 was about 3%, compared to 26% in 1976-77; the biomass of cyclopoids was 61% in September 2011 whereas in September 1976-77 no cyclopoids were recorded at approximately the same location (Keen and Potash 1978).

3.5.3. Selectivity

The Manly-Chesson Selectivity Index indicated that white perch were highly selective for large cladocerans in June and July of 2005, 2010 and 2011 (Figure 3.4). White perch were highly selective for *Daphnia* and other large cladocerans over cyclopoid copepods or small cladocerans in all months in which zooplanktivory was observed. White perch often had a majority of just one genus of zooplankton in their stomachs and small cladocerans or copepods were rarely found.

In 2010, alewife showed slight selectivity for cyclopoid and calanoid copepods throughout the summer. Alewife rarely selected either small or large cladocerans in higher proportions than those zooplankton were available to them (Figure 3.4). A different pattern was observed in alewife diet composition in 2011, when strong selectivity for both *Daphnia* and large cladocerans was observed in June, however these results were from a small sample size collected on only one date.

3.6. Discussion

The invasion of Missisquoi Bay, Lake Champlain by alewife does not appear to have strongly impacted the feeding behavior of the earlier invader, white perch. White

perch diet composition in 2010 and 2011 overall was consistent with that observed in 2005 (Couture and Watzin, 2008; Figure 3.2). White perch were highly omnivorous with phases of zooplanktivory that coincided with periods of *Daphnia* availability. In 2010, nearly all of the alewife collected had consumed exclusively zooplankton. Based on our results, zooplankton appeared to be an important prey item for alewife when they were grazing in Missisquoi Bay. Alewife were consuming the same resources as white perch, at least in June and July.

White perch in Missisquoi Bay showed a higher degree of zooplanktivory than in some other types of ecosystems. For example, in Virginia estuaries, adult white perch consumed mostly sand shrimp (St-Hilaire *et al.* 2002) and in a New Jersey coastal river system adult white perch diets were was comprised of primarily shrimp or amphipods (Weis 2005). In reservoirs of North Carolina, white perch ate mostly benthic invertebrates and little zooplankton or fish (Feiner *et al.* 2013). In inland and coastal Maine lakes, re-introductions of historically native alewife resulted in changes in white perch diet composition to include less zooplankton and more fish (Moring and Mink 2002) but our results did not indicate a similar trend in Missisquoi Bay. In Lake Erie, white perch diets have been similar to Lake Champlain, with periods of piscivory and zooplanktivory throughout summer months(Griswold and Tubb 1977, Schaeffer and Margraf 1986, Guzzo *et al.* 2013). White perch are highly opportunistic omnivores so differences among systems are not surprising. In shallow eutrophic lakes, prey switching by white perch among zooplankton, fish, and benthic invertebrates keeps predation pressure high on zooplankton (Jeppesen *et al.* 1997, Gopalan *et al.* 1998).

Alewife diet composition in Missisquoi Bay was consistent with studies from other lakes where large cladocerans were available (Smith 1970, Pothoven and Vanderploeg 2004, Walsh *et al.* 2012). An annual pattern of consumption of cyclopoid copepods in spring, *Daphnia* and other large cladocerans in summer and a return to cyclopoid consumption in the fall has been observed in Lake Ontario (Urban and Brandt 1993, Stewart *et al.* 2010), as well as inland lakes in Connecticut (Post *et al.* 2008) and New York (Wang *et al.* 2010). Alewife in Missisquoi Bay were not observed to consume large quantities of fish eggs or larval fish, which are two of the mechanisms by which alewife can be most damaging to native fish species (Madenjian *et al.* 2008).

Behavioral flexibility in alewife between particulate and filter feeding on zooplankton complicate assessments of their net impacts on the zooplankton community (Lazzaro 1987, MacNeill 1990). Our selectivity results seem to indicate of relatively non-selective feeding by alewife in 2010 (Figure 3.4). Alewife can cause lake-wide changes in zooplankton size structure in invaded lakes within several decades (Brooks and Dodson 1965, Wells 1970, Post *et al.* 2008). Several species of cladocerans have decreased in size throughout Lake Champlain since the arrival of alewife (Mihuc *et al.* 2012).

Despite extensive sampling effort in 2011, few adult alewife were caught. Their population was probably much more sparse in the bay that summer. High variability in alewife presence in Missisquoi Bay might be related to water temperature preferences. In summer months, temperatures in Missisquoi Bay are much higher than deeper sections of

Lake Champlain, where alewife populations are generally more abundant (Mihuc *et al.* 2012, Simonin *et al.* 2012).

YOY alewife and white perch were not extensively sampled in this study, but it is likely that they are also actively grazing on zooplankton and contributing to changes in community composition and size structure in Missisquoi Bay. Sampling in the western basin of Lake Erie indicated high temporal overlap in peak abundance of larval white perch and alewife from mid June to mid July (Gopalan *et al.* 1998). YOY ontogenetic diet shifts occur as a function of zooplankton size, availability and density (Prout *et al.* 1990) so fish can be affected by the annual declines in *Daphnia* and large cladocerans that occur in Missisquoi Bay. YOY white perch can switch to benthic prey at a much younger age compared to YOY alewife, which continue to consume primarily zooplankton (Parrish and Margraf 1990, Prout *et al.* 1990, Urban and Brandt 1993, Gopalan *et al.* 1998) so the period of highest diet overlap for prey among YOY will be limited in duration, similar to the adults.

The increase in total zooplankton biomass in Missisquoi Bay from the 1970s (Figure 3.3.) is probably a result of increased eutrophication of the bay that occurred in the same time frame (Levine *et al.* 2012), but the changes in zooplankton community composition and decreased relative abundance of the largest zooplankton taxa might be related to increased abundance of zooplanktivorous fish such as white perch. We observed a decrease in total zooplankton biomass from 2005 to 2010 and 2011, which might be related to the additional plankton grazing pressure by alewife.

Our data suggests that the compounding effects of both alewife and white perch selective planktivory might be one factor that leads to further reductions in large zooplankton biomass across all taxonomic classes. Large zooplankton regulate phytoplankton community composition by both direct consumption and by indirect stoichiometric mechanisms that affect nutrient recycling rates (Elser 1999). In eutrophic shallow lakes or bays such as Missisquoi Bay, the removal of large zooplankton by fish could enhance the likelihood that algal blooms will occur (Brett and Goldman 1997, Vanni *et al.* 1997, Dokulil and Teubner 2000).

In Missisquoi Bay, white perch are highly selective for large cladocerans among the zooplankton community. Alewife exacerbate the feeding pressure of white perch on the zooplankton community by consuming large cladocerans, as well as smaller zooplankton. Compared to historical conditions, *Daphnia* and other large zooplankton have declined in abundance and overall biomass in Missisquoi Bay. Both alewife and white perch consume large zooplankton, so they might be contributing to long-term changes in the zooplankton community.

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Table 3.1: Categories used for the classification of the stomach contents of white perch and alewife.

Zooplankton	Other
Small Cladocerans	Arthropods
Alona bicolor	Amphipoda
Bosmina longirostris	Coleoptera
Ceriodaphnia lacustris	Diptera
Chydorus sphaericus	Ephemeroptera
Eubosmina coregoni	Isopoda
Cyclopoid Copepods	Odonata
Acanthocyclops vernalis	Trichoptera
Cyclops scutifer	Other Benthos
Diacyclops thomasi	Annelida
Eucyclops spp.	Hirudinea
Mesocyclops edax	Bivalvia
Thermocyclops spp.	Gastropoda
Daphnia	Eggs
Daphnia galeata mendotae	Non-animal matter
Daphnia longiremis	Fish
Daphnia pulex	
Daphnia retrocurva	
Large Cladocerans	
Diaphanosoma birgei	
Holopedium gibberum	
Leptodora kindtii	
Calanoid Copepods	
Epishura lacustris	
Leptodiaptomus/Skistodiaptomus	

Table 3.2: Average monthly diet composition by abundance in fish sampled in 2005 (Couture and Watzin 2008) and April 2010 - September 2011 (this study). Sample size (N) is the number of fish with identifiable stomachs contents; TL (total length, mm ± SE); Weight (g ± SE); Zoop includes zooplankton; Benthos includes benthic arthropods; Other includes eggs, mollusks, and non-animal matter. Non-zero frequencies below one tenth of a percent are indicated by <0.1.

Year	Species	Month	N	Length	Weight	% Abundance			
						Zoop	Benthos	Other	Fish
2005	White perch	April	20	230 ± 5	198 ± 17	0	94	6	<0.1
		May	9	226 ± 9	189 ± 26	0	92	8	0
		June	75	220 ± 3	167 ± 7	93	7	<0.1	<0.1
		July	100	215 ± 3	161 ± 7	9	86	2	3
2010	White perch	April	46	256 ± 6	291 ± 21	0	91	8	1
		May	25	232 ± 7	199 ± 20	<0.1	98	2	0
		June	46	224 ± 5	168 ± 11	39	56	4	1
		July	92	235 ± 4	199 ± 10	22	62	10	5
		August	83	242 ± 5	226 ± 14	1	72	9	18
		September	6	224 ± 31	207 ± 59	6	54	6	34
	Alewife	May	21	238 ± 4	110 ± 6	95	3	<0.1	0
		June	25	181 ± 8	63 ± 8	76	18	<0.1	0
		July	15	142 ± 5	38 ± 3	100	0	0	0
		August	21	133 ± 6	28 ± 3	54	46	0	0
		September	8	115 ± 13	17 ± 7	100	0	0	0
2011	White perch	April	2	183 ± 2	96 ± 0	0	99	1	0
		May	28	206 ± 6	131 ± 16	2	83	11	4
		June	139	233 ± 3	197 ± 8	33	49	5	14
		July	29	246 ± 8	248 ± 25	46	18	5	31
		August	61	232 ± 5	205 ± 14	0	37	10	53
		September	18	219 ± 15	190 ± 27	0	74	5	21
	Alewife	June	11	175 ± 6	49 ± 7	100	<0.1	0	<0.1
		September	2	96 ± 5	8 ± 1	88	13	0	0

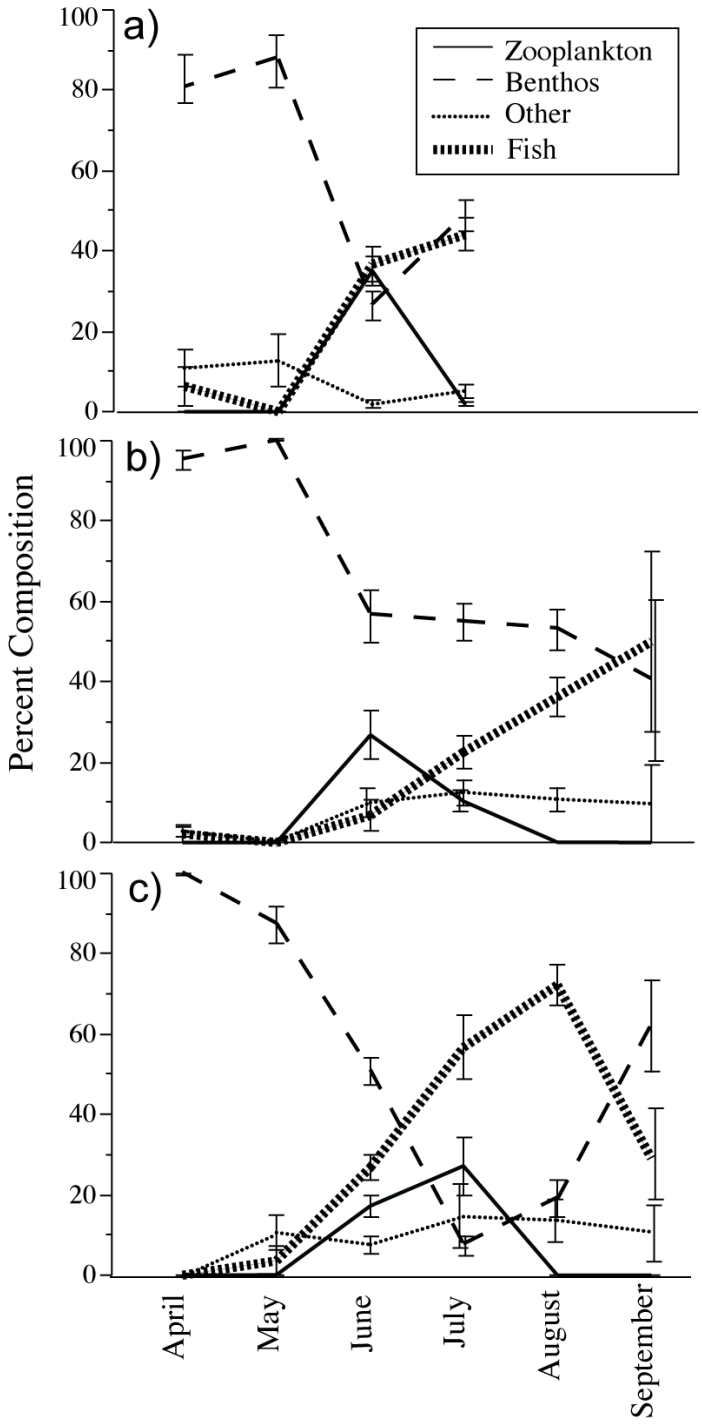

Figure 3.1: Mean monthly percent composition of white perch diet composition by dry weight of prey items in (a) 2005 (Couture and Watzin 2008), (b) 2010, and (c) 2011 in Missisquoi Bay, Lake Champlain. Benthos includes benthic arthropods; Other includes eggs, mollusks, and non-animal matter.

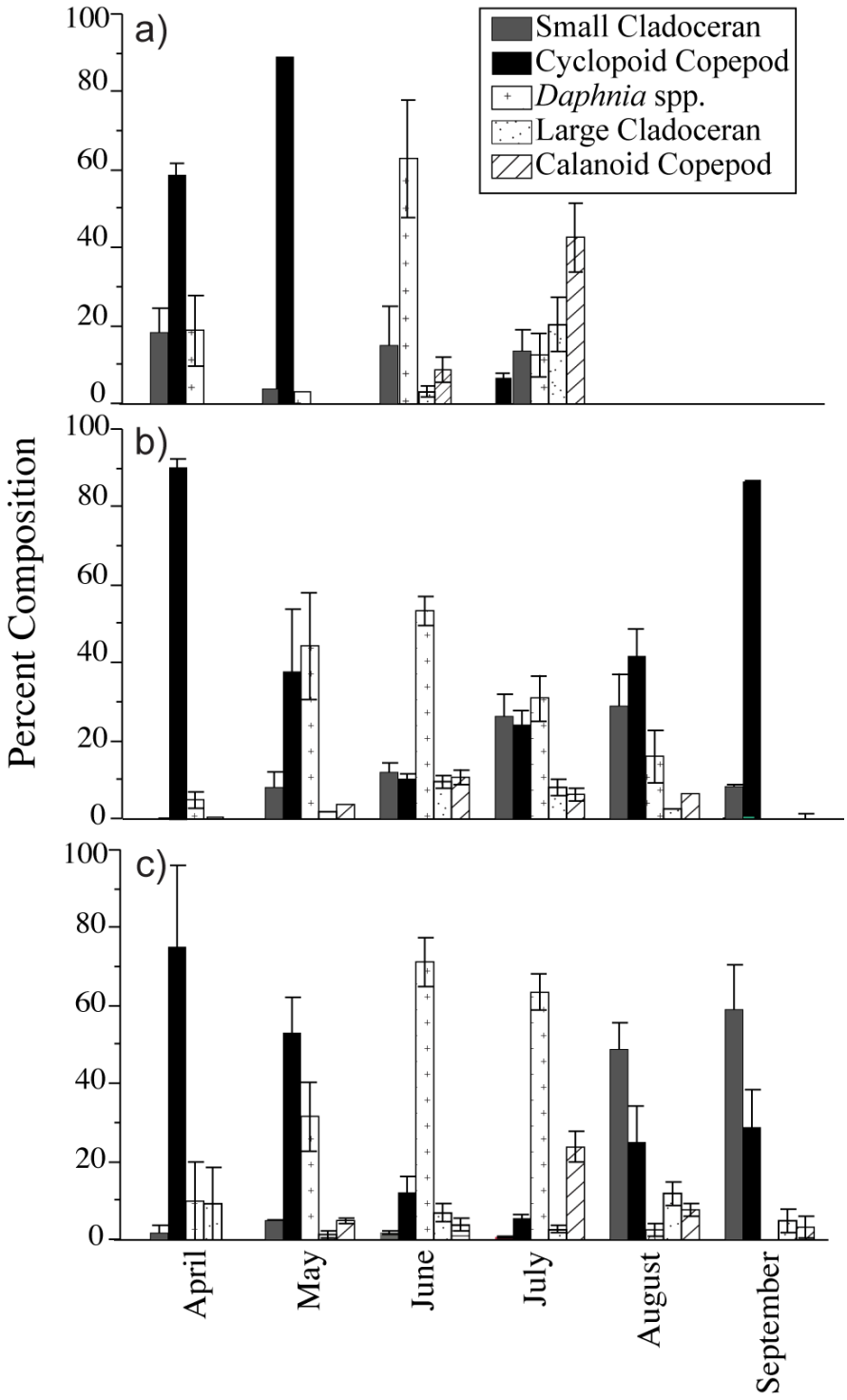

Figure 3.2: Mean monthly percent community composition by abundance of ambient zooplankton (± SE) in (a) 2005 (Couture and Watzin 2008), (b) 2010, and (c) 2011 in Missisquoi Bay, Lake Champlain.

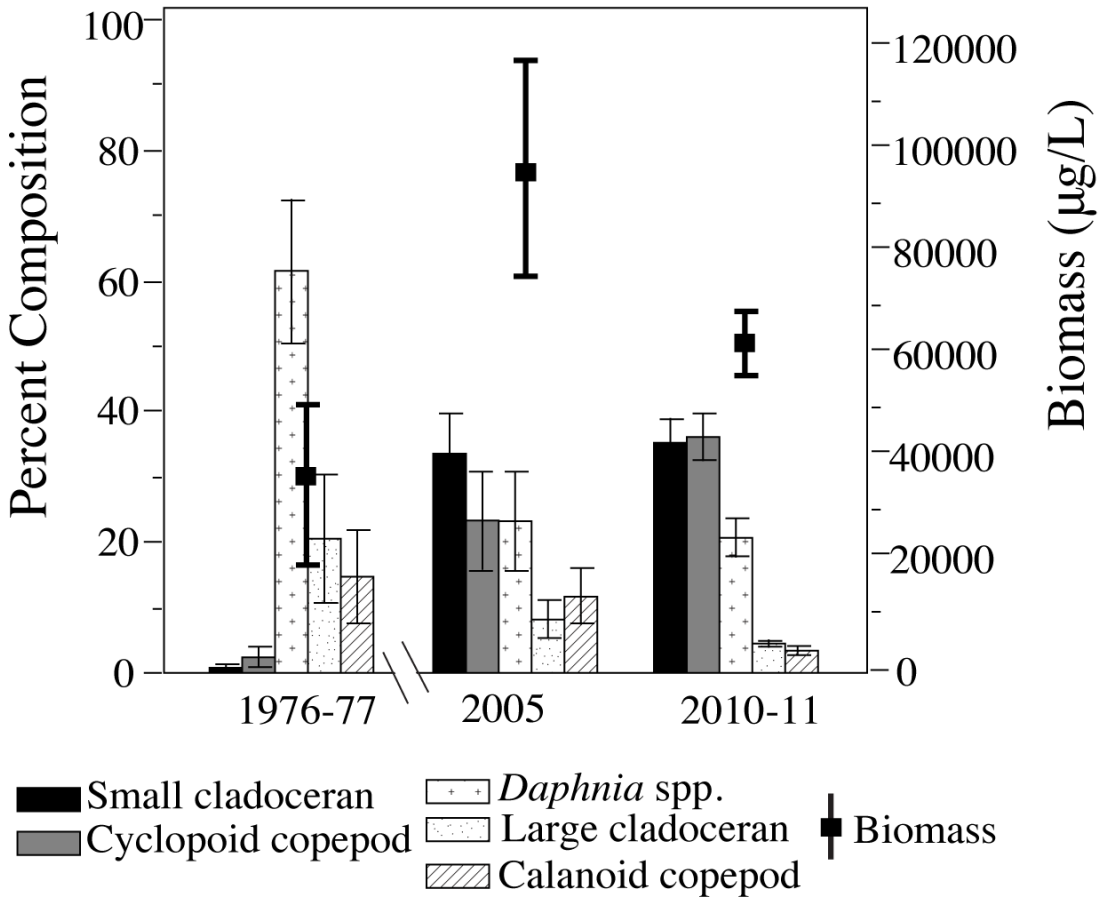

Figure 3.3: Mean annual zooplankton community percent composition (± SE, left axis) and total biomass (± SE, right axis) in 1976-77 (Keen and Potash 1978), 2005 (Couture and Watzin 2008), and 2010-2011 (this study).

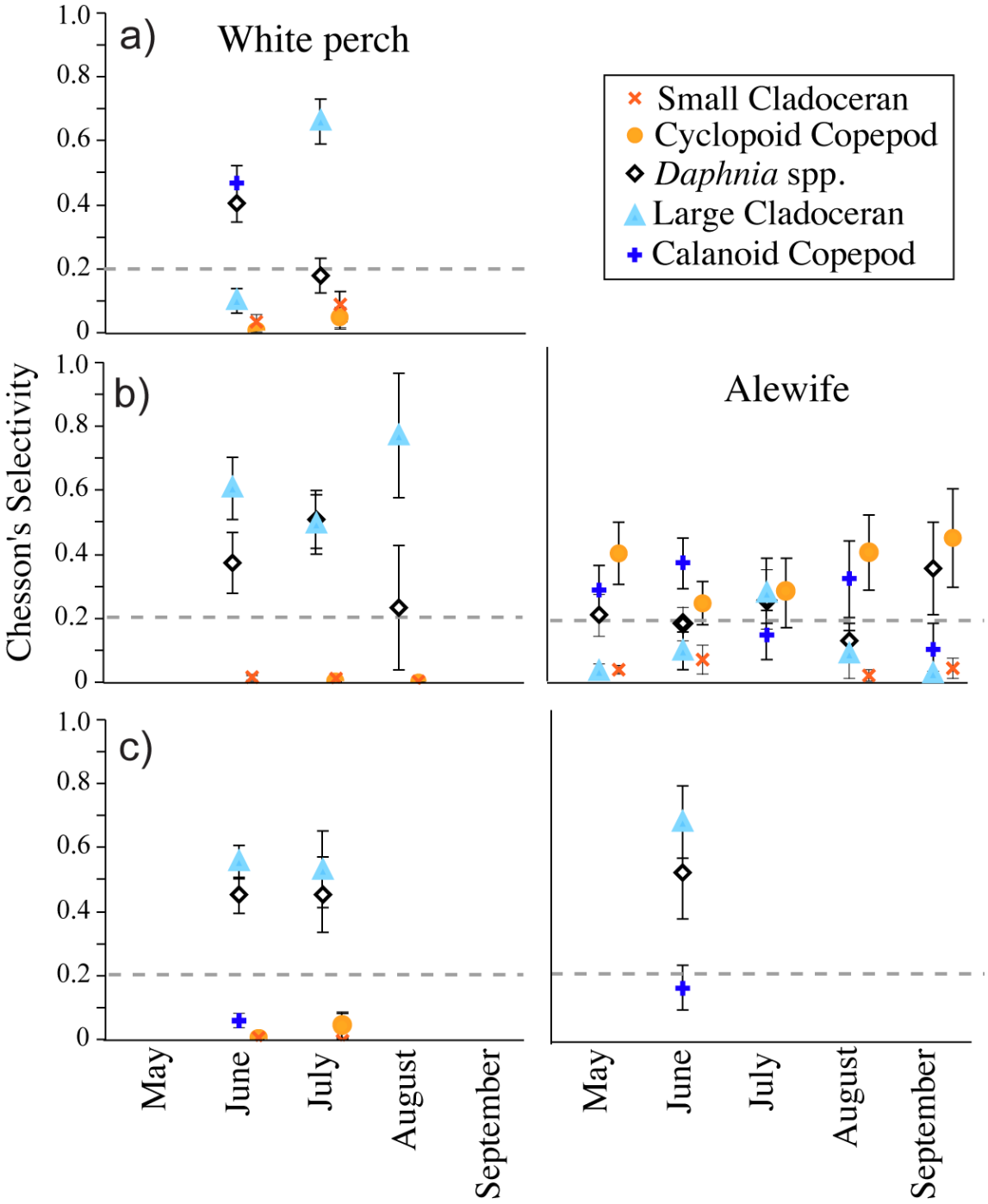

Figure 3.4: Mean monthly selectivity values (Manly Chesson selectivity index ± SE) for zooplankton groups in a) 2005 (Couture and Watzin 2008), b) 2010, and c) 2011. Broken line indicates neutral selectivity value (m^{-1}; 0.2). Monthly samples consisting of less than three fish were not included. Alewife were not collected in Missisquoi Bay in 2005.

CHAPTER 4: EVALUATION OF ZOOPLANKTON GRAZING AND CYANOBACTERIA BLOOMS.

4.1. Abstract

High nutrient concentrations are one factor associated with the development of cyanobacteria blooms in eutrophic lakes, but interactions between zooplankton grazers and shifts in phytoplankton community composition remain to be fully tested. Invasive planktivorous fish predation on large zooplankton can create the potential for cascading responses in phytoplankton. We evaluated the phytoplankton response in Lake Champlain to changes in the zooplankton community that have been linked to fish selective grazing pressure. In mesocosms, we established treatments with enhanced or reduced quantities of large zooplankton in 10-day trials (July and August 2011, May 2012). To isolate the interactions of zooplankton biomass and phytoplankton response, only zooplankton were manipulated in our treatments. Treatment effects were most apparent in the May trial when cyanobacteria was not the dominant type of phytoplankton. Large zooplankton biomass was associated with higher abundances of small-cell cyanobacteria and grazing-resistant taxa. In the July trial when a dense cyanobacteria bloom was underway, there were no treatment effects. In the August trial, the presence of large zooplankton led to a higher abundance of edible phytoplankton. The results of this study show that zooplankton grazing influences phytoplankton community composition, particularly in early summer. In our mesocosms, the strength of this interaction changed when the phytoplankton assemblage became dominated by

cyanobacteria. Consideration of the impacts of zooplankton grazing must be part of any assessment or management plan for eutrophic shallow lakes prone to cyanobacteria blooms.

4.2. Keywords

Zooplankton, Phytoplankton, Mesocosms, Cyanobacteria, Lake Champlain

4.3. Introduction

Cyanobacteria blooms in shallow eutrophic lakes have been linked to numerous ecological processes (Hyenstrand *et al.* 1998). The mechanisms that trigger blooms and those that maintain blooms are not likely the same (Scheffer *et al.* 2003). Several known conditions that lead to the initiation of blooms of grazing-resistant and potentially toxic cyanobacteria include: high nutrient levels, low N:P ratio, warm temperatures, high water column stability, and limited zooplankton grazing (Scheffer *et al.* 1997, Elser 1999, Dokulil and Teubner 2000, Downing *et al.* 2001). Understanding the mechanisms by which one kind of phytoplankton comes to dominate the community composition, particularly cyanobacteria, is valuable for the management of public health risks through exposure to potentially toxic blooms (Chorus *et al.* 2000).

Several characteristics of cyanobacteria that favor their success over other types of phytoplankton include buoyancy regulation, high temperature tolerance, superior ability to store nutrients, low irradiant light requirements, resistance to zooplankton grazer pressure, and higher competitive capabilities for trace elements and limiting nutrients (Scheffer *et al.* 1997, Hyenstrand *et al.* 1998, Reynolds 1998). High total

nutrients and a low N:P ratio are often associated with blooms of nitrogen-fixing cyanobacteria or other types of cyanobacteria that more readily use reduced forms of nitrogen such as ammonia (Smith 1983, Downing *et al.* 2001, Schindler 2012). Although high nutrient levels are often associated with blooms, the presence of eutrophic conditions does not guarantee that a cyanobacteria bloom will occur (Downing *et al.* 2001). There are interactions between nutrient availability and trophic dynamics that are likely to determine phytoplankton community composition (Gliwicz 1990, Elser 1999, Schindler 2006).

Zooplankton grazing appears to be most important in shaping phytoplankton community structure in early summer, before cyanobacteria blooms become dense (Hambright and Hall 1992). *Daphnia* are size-selective filter feeders and are most likely to control blooms when cyanobacteria densities are low (Gliwicz 1990, Hambright *et al.* 2007a). *Daphnia* are able to directly slow bloom development by grazing individual cells and small colonies of cyanobacteria (Sarnelle 1993, Vanni and Layne 1997, Bell 2002). Laboratory experiments have shown that once a bloom is underway, the growth rates achieved by cyanobacteria and the presence of large colonies interferes with *Daphnia*'s ability to efficiently graze on cyanobacteria (Gliwicz 1990). The specifics of the interplay of nutrient concentrations and algal response to alterations in zooplankton grazer community composition however, are not well known (Vanni and Layne 1997, Elser 1999).

Zooplankton community composition impacts phytoplankton competition through both direct and indirect mechanisms, (Vanni and Layne 1997, Elser 1999).

Indirectly, changes in zooplankton community composition can alter nutrient recycling rates through physiological differences in the stoichiometry of large and small zooplankton (Hambright *et al.* 2007b). Compared to *Daphnia*, copepods and small cladocerans differ in both their filter feeding rates, food size selection and the ratio of excreted N and P (Gliwicz 1990, Vanni *et al.* 1997). Large zooplankton accumulate P in their body tissues and their waste is comprised of a higher N:P ratio than small zooplankton. In addition to direct grazing mortality, such alterations in nutrient supply ratios can contribute to conditions that favor development of cyanobacteria blooms (Sterner and Elser 2002).

Directly, predation on zooplankton by fish can reduce the biomass of large zooplankton, which decreases grazing pressure on the phytoplankton community (Brooks and Dodson 1965, Hambright and Hall 1992, Jeppesen *et al.* 1997). Size-selective grazing by invasive planktivorous fish can lead to long-term declines in large cladocerans and increases in smaller zooplankton (Wells 1970, McQueen *et al.* 1989, Wang *et al.* 2010). In Lake Champlain, diet studies of invasive white perch (*Morone americana*) and alewife (*Alosa pseudoharengus*) have shown selective consumption of large zooplankton, especially large cladocerans, such as *Daphnia* and *Leptodora*. An annual period of planktivory by adult white perch occurs primarily in June and July, followed by a decline in large zooplankton biomass (Couture and Watzin 2008, R. Gorney *unpublished data*). Throughout shallow bays of the lake, the composition of the zooplankton community has shifted to be comprised of more small taxa (Mihuc *et al.* 2012), while cyanobacteria

blooms have become more common (Smeltzer *et al.* 2012), but the link between the two has not been clearly demonstrated.

Changes in trophic dynamics are difficult to predict because the link between zooplankton and phytoplankton is mediated both by nutrient supply and the presence of fish (McQueen *et al.* 1989, Brett and Goldman 1997). As evidence of this complexity, experimental and observational studies of zooplankton grazing pressure have shown inconsistent responses by phytoplankton (Brett and Goldman 1996, Vanni *et al.* 1997, Weis and Post 2013). Mesocosm studies that manipulated combinations of nutrient concentrations and more than one trophic level such as planktivorous fish biomass or individual species of zooplankton, led to responses that were difficult to interpret (Carpenter *et al.* 2001, Bell 2002, Spivak *et al.* 2011). In this study, we manipulated only the zooplankton community composition to attempt to isolate the effects of large zooplankton biomass on phytoplankton community structure. Few previous studies have focused in this way.

The goal of our study was to use manipulations in mesocosms to evaluate the response of phytoplankton community composition to changes in the density and composition of zooplankton that occurs as a result planktivory by invasive fish in Missisquoi Bay, Lake Champlain. We conducted three trials (July and August 2011, and May 2012) in which we compared phytoplankton response to grazing pressure both prior to and during a cyanobacteria bloom. We hypothesized that in treatments where large zooplankton biomass was increased, cyanobacteria and other grazing-resistant phytoplankton would decrease in biovolume because of higher grazing pressure.

4.4. Methods

4.4.1. Study Site and Zooplankton Treatment Creation

Lake Champlain is a long (193 km), narrow (maximum width 20 km) lake that lies on the border between Vermont and New York and extends north into Quebec, Canada (Figure 4.1). The mesocosms were located on the shore of Missisquoi Bay, at the northern extent of the lake (44° 59.54'N, 73° 10.46'W, Figure 4.1). The eutrophic bay (surface area 77.5 km^2) is uniformly shallow (average depth 3 m, maximum depth 4 m) with dense annual cyanobacteria blooms and established populations of invasive planktivorous fish (Couture and Watzin 2008, Smeltzer *et al.* 2012, Watzin *et al.* 2012).

We conducted three 10-d trials in July and August 2011 and May 2012 in 16 - 200 L, semi-translucent polyethylene plastic barrels (0.95 m high x 0.55 m dia) arranged in a square array onshore. The mesocosms were covered with 5 cm mesh netting to keep out foreign debris. Prior to the start of each trial, all mesocosms were filled with water pumped from approximately 50 m from shore at a water depth of 0.5 m from the surface using an enclosed-impellor, low-speed pump. The water was filtered (250 μm sieve) to reduce initial density of zooplankton in the mesocosms. The phytoplankton community was not manipulated.

Zooplankton for the mesocosms was collected from a nearby, offshore site in Missisquoi Bay (Figure 4.1) where cyanobacteria blooms have historically been densest (Watzin *et al.* 2012). Zooplankton was collected in multiple 3 m vertical tows with a 30 cm dia, 363 μm mesh zooplankton net. The number of tows was adjusted in each trial

based on the ambient density of zooplankton biomass estimated from visual inspection of the collections in the field. In our original 2 x 2 factorial design, we planned to create high and low density levels of both large and small zooplankton using a 420 μm sieve to separate size classes of zooplankton and multiple vertical plankton net tows. For the "*Big*" treatments, large zooplankton collected on the sieve were added into mesocosms in high or low density (n = 4 of each). For the "*Small*" treatments, high and low densities of the zooplankton passing through the sieve were added to the mesocosms. Unfortunately, we were not successful in creating discrete density levels of either zooplankton size class so our treatments were condensed into a single factor experiment (*Big* and *Small* size) with varying densities of large and small zooplankton across eight replicates.

Phytoplankton and zooplankton samples were collected from every mesocosm on Day 1, Day 3 and Day 10 of each trial. A 2 L Van Dorn sampling bottle was used to collect water from the middle of the mesocosms after gentle stirring to evenly distribute any organisms. Whole-water phytoplankton samples (50 mL) were preserved with 1% acid Lugol's solution. For zooplankton collection, 2 L of sampled mesocosm water were filtered (Nitex 80 μm filter) and preserved in 70% ethanol (APHA 1998). All samples were collected in triplicate.

4.4.2. Sample Analysis

Phytoplankton were enumerated by use of the Ütermohl technique. An aliquot was settled for at least 24 h in a vertical settling chamber and examined using inverted microscopy at 400X (APHA 1998). Samples were identified to at least genus level

(Prescott 1982). Cell counts and colony size structure were recorded. Abundances (cells mL^{-1}) were calculated for all taxa. The total abundances of the most common genera (comprising ≥ 1 % of total cell abundance) were converted to biovolume (μm^3 ml^{-1}) using median values of measured linear dimensions of Lake Champlain phytoplankton (A. Shambaugh, *unpublished data*) and geometric formulae (Hillebrand *et al.* 1999). All phytoplankton genera were classified into six major taxonomic groups: small-cell groups (which included small non-colony forming cyanobacteria such as *Chroococcus* and *Synechococcus*), colony-forming cyanobacteria, diatoms (Bacillariophyceae), chlorophytes, cryptophytes, and chrysophytes (non-diatom).

Published classifications were used to determine biovolume fractions of the phytoplankton biovolume comprised of edible and grazing-resistant phytoplankton (Sarnelle 1993, Seip and Reynolds 1995, Agrawal 1998, Reynolds *et al.* 2002). The edible portion contained all cryptophytes, chrysophytes, and some chlorophytes. Cyanobacteria, small-cell groups, large chlorophytes, and diatoms were considered grazing-resistant because of large size, gelatinous sheaths, or in the case of diatoms, siliceous outer walls. For a more detailed analysis of community composition, Shannon diversity (H) and generic richness were calculated using cellular abundance for each mesocosm on each sample date (Hill 1973).

Zooplankton were identified and classified into five major taxonomic groups: calanoid copepod, cyclopoid copepod, *Daphnia* spp., small cladocerans, and other large cladocerans. A threshold (~1 mm) average medial axial length measurement was used to separate the major zooplankton taxonomic groups as either "large" or "small."

The large group included calanoid copepods, *Daphnia* spp., and other large cladocerans (including the species *Diaphanosoma birgei*, *Holopedium gibberum*, and *Leptodora kindti*). The small group included cyclopoid copepods and all small cladocerans (including the species *Bosmina longirostris*, *Eubosmina coregoni*, *Ceriodaphnia lacustris*, and *Alona bicolor*). If abundances in a sample were greater than about 400 organisms, a random subsample was examined and counting proceeded until at least 200 organisms (± 20 %) were identified. Lengths of 100 individuals of each major taxonomic group were recorded from each trial. Zooplankton biomass (μg m^{-3}) was calculated based on published length-weight regression equations, average lengths, and densities observed within the mesocosms (Downing and Rigler 1984).

4.4.3. Data Analysis

For all analyses, zooplankton biomass and phytoplankton data were log (x+1) transformed to stabilize variances. Initial treatment differences in zooplankton biomass were compared using a one-way analysis of variance (ANOVA). We calculated the ratio of large to small zooplankton biomass within the treatments on Day 1 to improve our ability to compare the treatments across trials. We compared initial phytoplankton community composition and zooplankton biomass between treatments with ANOVA followed by a Bonferonni multiple comparisons test.

To evaluate the effect of zooplankton grazing pressure among all three trials we compared phytoplankton response variables using repeated-measures ANOVA (RM-ANOVA). Two main effects were included in the model to account for within- and

among-trial variation: the repeated sampling measure (sample day) and trial. We tested phytoplankton response within each trial over time as a response to the measured biomass of zooplankton in the mesocosms on each sampling day. Biomass of large and small zooplankton in the mesocosms on each sampling day was included in the RM-ANOVA as two time-varying covariates. The final model included the two time effects (day and trial), the biomass covariates, and an interaction term. The phytoplankton response variables included were commonly measured aspects of phytoplankton community structure: abundance (cells mL^{-1}) of small-cell groups, cyanobacteria, diatoms, chlorophytes, and cryptophytes, biovolume (μm^3 mL^{-1}) of grazing-resistant or edible phytoplankton, generic richness, and diversity.

Measures of the phytoplankton community that had a statistically significantly response to large or small zooplankton biomass in the overall RM-ANOVA were selected for further analyses. We conducted an additional RM-ANOVA for each trial and included a fixed effect of the *Big* and *Small* treatments, rather than the zooplankton biomass covariates. Paired t-tests were used to test for differences in phytoplankton response among sample days within a trial. The initial RM-ANOVA was run using *proc mixed* in SAS Version 9.3 (SAS Institute, Inc., Cary, NC) and all other analyses were conducted in JMP Pro 10.0 (SAS Institute, Inc., Cary, NC).

4.5. Results

4.5.1. Treatment Creation

On Day 1 of all three trials, the ratio of large to small zooplankton biomass was higher in the *Big* treatments (ANOVA, $p < 0.001$), however, the biomass of zooplankton introduced into the mesocosms varied among the trials (Table 4.1). On Day 1 of every trial, large zooplankton comprised greater than 50% of the total zooplankton biomass in the *Big* treatments. In the May trial there was higher biomass of small zooplankton in the *Small* treatments than in the *Big* treatments (ANOVA, May: $p = 0.005$, Table 4.1). In the July and August trials, there was no difference in biomass of small zooplankton between the *Big* and *Small* treatments.

In the May trial, *Daphnia* comprised 54% of total zooplankton biomass in the *Big* treatments and 5% in the *Small* treatments (Figure 4.2). The mean composition of small zooplankton biomass in the *Small* treatments on Day 1 was over 90%. Total zooplankton biomass was highest in the May trial (Table A.1). In the July trial, total large zooplankton biomass was comprised primarily of calanoid copepods (44%) and *Daphnia* (28%) in the *Big* treatments. In the *Small* treatments, the community was comprised of mostly small zooplankton (51%), some calanoid copepods (5%), and *Daphnia* (32%). For the August trial, total zooplankton biomass was comprised primarily of calanoid copepods (20%) and large cladocerans of the family Sididae (25%). Total mean percent composition of large zooplankton in the *Big* treatments (60%) was higher than in the *Small* treatments (17%, ANOVA, $p = 0.031$, Figure 4.2).

On Day 1, the abundance of major phytoplankton taxonomic groups did not differ between *Big* and *Small* treatments in any of the trials (Figure 4.3). At the start of the May trial, the phytoplankton community was comprised of primarily of cryptophytes such as *Cryptomonas* and *Chroomonas*, typical of spring conditions in temperate eutrophic lakes. At the start of the July trial, cyanobacteria comprised about 97% of the total phytoplankton abundance, although non-cyanobacteria groups were still present. The cyanobacteria was dominated by three common genera: *Microcystis*, *Aphanizomenon*, and *Anabaena*. At the start of the August trial, a dense cyanobacteria bloom was still underway. Small-cell phytoplankton groups were common and non-cyanobacteria taxa were rare.

4.5.2. Phytoplankton Response to Zooplankton Treatments

In the overall RM-ANOVA, the response of almost all of the phytoplankton variables was strongly related to trial or day of measurement (Table 4.2). Mean total phytoplankton biovolume within the mesocosms increased during the May and July trials and remained constant in the August trial. The proportion of the total biovolume that was comprised of grazing-resistant phytoplankton increased over time within each trial, as biomass of large zooplankton declined. Grazing-resistant phytoplankton and generic richness both increased as a response to interactions between small and large zooplankton biomass (Table 4.2).

The results of the overall RM-ANOVA guided the selection of five of the phytoplankton response variables to include in the additional analyses. In separate RM-

ANOVAs by trial, the responses of those phytoplankton response variables to *Big* and *Small* treatment levels were examined (Table 4.3). Sample day had an effect on the abundance of phytoplankton across both *Big* and *Small* treatments in all three trials. In the May trial, the abundance of small-cell phytoplankton differed by treatment (ANOVA, $p = 0.021$) but the interaction term was also significant. One-way ANOVAs indicated no change in abundance of small-cell phytoplankton in the *Big* treatments and a decrease in the *Small* treatments (ANOVA, $p = 0.001$) throughout the course of the trial (Figure 4.4).

There was an increase in grazing-resistant phytoplankton over the course of the May trial in both treatments (ANOVA, $p < 0.001$). The largest increase in biovolume occurred between Day 3 and Day 10 in the *Small* treatments (Figure 4.4). Large, grazing-resistant phytoplankton taxa, such as colonial cyanobacteria and large diatoms, comprised the majority of the phytoplankton community present in both treatments by Day 10. The mean abundance of large diatoms increased in the *Big* treatments and was higher on Day 10 (t-test: $t = 2.08$, $df = 2$, $p < 0.005$).

In the July trial, no treatment effects were detected in the RM-ANOVA (Table 4.3). The small-cell phytoplankton significant interaction between sample day and treatment can be related to a higher initial abundance of these groups in the *Big* treatments. The response did not differ between the treatments (Figure 4.4). In the August trial, edible phytoplankton response was different between the treatments (Table 4.3). Over the course of the August trial there was a decline in edible phytoplankton in the *Small* (ANOVA, $p = 0.046$) but not in the *Big* treatments.

4.6. Discussion

We found that the response of phytoplankton to manipulations of zooplankton grazer size structure was slightly different among the three trials. Trophic links between phytoplankton and zooplankton in our mesocosms were most apparent in the May trial, prior to the dominance of the phytoplankton community by grazing resistant cyanobacteria. At that time, zooplankton grazing had the strongest impact on phytoplankton community composition, leading to changes in the abundance of several functional groups and increased generic richness. In the July and August trials, once the phytoplankton community was dominated by large colonies of cyanobacteria, large zooplankton were not able to reduce grazing-resistant phytoplankton biovolume in either *Big* or *Small* treatments. However, in those trials, the total zooplankton biomass, and thus grazing pressure, was also lower.

In each of the three trials of this study, we were able to create distinct zooplankton assemblages (Figure 4.2) in on-shore mesocosms that, at least in part, mimicked the impacts of fish planktivory. The *Small* treatment mesocosms in each trial contained higher biomass of small taxa, particularly small cladocerans and cyclopoid copepods, both of which tend to increase in lakes with high levels of selective planktivory by fish (Brooks and Dodson 1965, Jeppesen *et al.* 2004, Wang *et al.* 2010). The *Big* treatments contained higher biomass of large zooplankton such as *Daphnia* and calanoid copepods, which are generally more abundant at lower levels of planktivory (Carpenter *et al.* 2001).

Trophic cascade theory predicts that an increase in a predator trophic level will lead to a reduction in herbivore populations with resulting cascading responses in the primary producers (Paine 1980, Carpenter *et al.* 1985, Carpenter *et al.* 2001). Evidence of top-down influence of zooplankton on phytoplankton in temperature eutrophic lakes is well supported (Leibold 1989, Sarnelle 1993, Jeppesen *et al.* 2004). Trophic status and nutrient availability can potentially mask the influence of cascading, top-down predator control (Hambright *et al.* 2007b). By manipulating zooplankton biomass and not nutrient enrichment in our mesocosm study, any changes in phytoplankton composition is sensitive are more clearly linked to zooplankton.

In our study, grazing-resistant phytoplankton biovolume increased in all three trials in both the *Big* and *Small* treatments. In the May trial, cyanobacteria abundance in both treatments was kept low for several days before increasing along with other grazing-resistant phytoplankton groups at the end of the trial (Figure 4.4). In the July and August trials, when bloom-level densities of grazing-resistant phytoplankton were already present, the zooplankton were not able to reduce cyanobacteria and other grazing-resistant phytoplankton in either treatment. Total zooplankton biomass and thus grazing pressure was also lower in the July and August trials than in the May trial.

Our results suggest that the timing of zooplankton removal has an effect on trophic dynamics, as has been hypothesized by others (Sarnelle 1993, Elser 1999). Selective grazing on large zooplankton by invasive fish in early summer can decrease the likelihood that grazing by zooplankton will curb seasonal blooms. Declines in zooplankton size and biomass can allow cyanobacteria blooms to continue or intensify

and may make restoration of previous ecological conditions increasingly difficult in the future (Van de Bund *et al.* 2004, Scheffer and van Nes 2007, Wang *et al.* 2010).

Models predict that the impacts of climate change will disproportionately affect shallow lakes and pervasive cyanobacteria blooms are likely to continue in future decades (Paerl and Huisman 2008, Kosten *et al.* 2012). Climate change and lake warming will likely interact with food web perturbations in Missisquoi Bay and could reduce the likelihood of bloom reduction by zooplankton grazing. The implications of climate and temperature change for phytoplankton and zooplankton population dynamics are likely to be most disruptive in spring, as the timing of interactions shifts across all trophic levels (Shurin *et al.* 2012, Wagner *et al.* 2013); though others argue that shifts in timing will occur similarly across trophic levels (Hansson *et al.* 2013).

Carefully designed mesocosm studies can be used to replicate the physical, chemical, and biological conditions and dynamics of the ambient environment (Van de Bund *et al.* 2004, Spivak *et al.* 2011). Fish and zooplankton influence the likelihood of cyanobacteria dominance by direct and indirect mechanisms. In addition to direct grazing impacts, zooplankton have stoichiometric effects on nutrient recycling processes and biogeochemical functions of lakes (Schindler *et al.* 1997, Vanni *et al.* 1997, Elser 1999). In Missisquoi Bay, shallow depths, high nutrient loads, and low N:P ratio all enhance the role of foodweb feedbacks, increasing the likelihood of dominance by cyanobacteria.

Changes in the zooplankton community caused by the selective grazing of invasive planktivorous fish can change grazing-induced mortality among phytoplankton

and favor grazing-resistant phytoplankton (Elser 1999, Schindler 2006, Hambright *et al.* 2007b). Despite challenges to the execution of our planned design, our study did yield valuable results concerning the interactions of zooplankton grazing pressure and phytoplankton community composition. The results of this study suggest that zooplankton grazing does influence phytoplankton community composition, particularly in early summer and when total zooplankton biomass is highest and before cyanobacteria becomes dominant in the phytoplankton community.

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4.8. References

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Table 4.1: Mean biomass (mg m^{-3} ± SE) of large and small zooplankton and ratio of large to small zooplankton biomass (± SE) in *Big* and *Small* treatments (n = 8 of each) on Day 1 of all three trials.

		Large Zooplankton		Small Zooplankton		Ratio (Large:Small)	
Trial	Treatment	Mean	SE	Mean	SE	Mean	SE
May	*Big*	879.5	171.5	598.8	84.2	1.7	0.4
	Small	76.7	25.5	754.6	77.7	0.1	0.1
July	*Big*	84.0	20.4	9.5	0.7	8.9	2.0
	Small	15.0	2.5	17.5	5.7	1.3	0.3
August	*Big*	150.3	52.8	49.9	13.5	3.5	1.3
	Small	10.8	2.3	93.5	38.4	0.2	0.1

Table 4.2: Results of the repeated measures ANOVA with large and small zooplankton biomass as continuous time-varying covariates across three trials. All mesocosms (n = 16 per trial) were sampled on Days 1, 3, and 10. Only significant results ($p < 0.05$) results are shown. Chryso. is chrysophytes; Chloro. is chlorophytes; Crypto. is cryptophytes.

	Response Variables									
Model Variables	Small-Cell	Cyano-bacteria	Grazing-Resistant	Edible	Richness	Diversity	Chryso.	Chloro.	Crypto.	Diatoms
Trial	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001		
Day		0.029	<0.001	<0.001	<0.001	<0.001	0.007		0.027	<0.001
Biomass (Lg.)			0.002							
Biomass (Sm.)	0.013									
Large*Small			0.001	0.044	0.011					

Table 4.3: Repeated measures ANOVA testing response of phytoplankton variables in *Big* and *Small* treatments (n = 8 of each) in each trial. Only significant results ($p < 0.05$) are shown.

Trial	Cyano-bacteria	Grazing-Resistant	Edible	Small-Cell	Richness
May					
Day	<0.001	<0.001	<0.001	0.001	<0.001
Treatment		0.024		0.018	
Day*Trmt				0.011	
July					
Day		<0.001	<0.001	<0.001	<0.001
Treatment					
Day*Trmt				0.036	
August					
Day	0.009	0.009			
Treatment			0.019		
Day*Trmt					

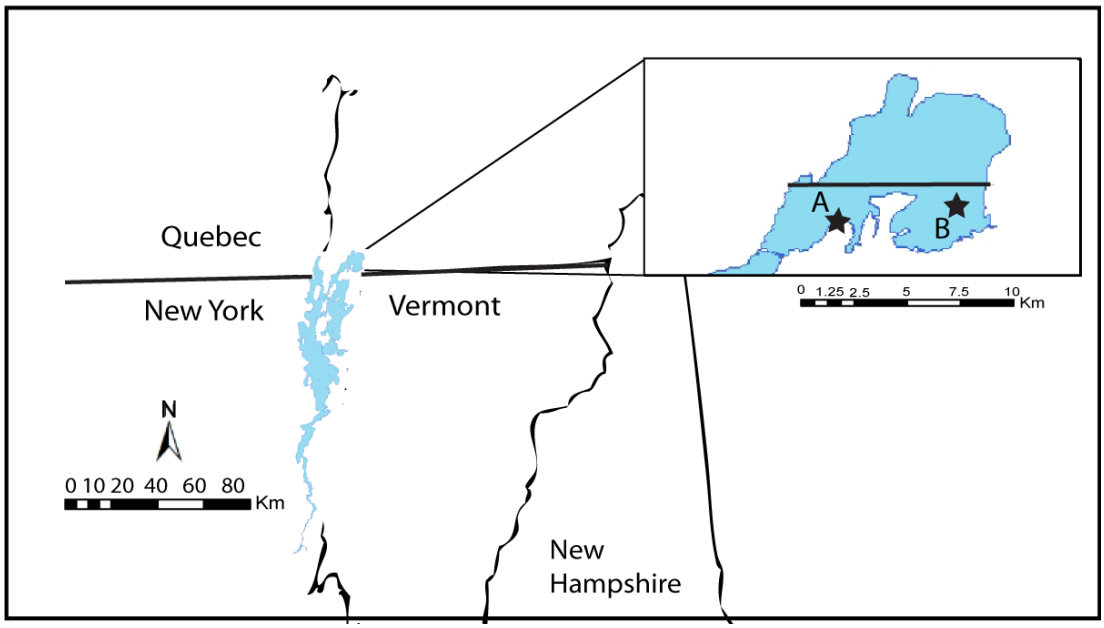

Figure 4.1: Lake Champlain with inset showing the study site, Missisquoi Bay, and location of (A) the mesocosms and (B) the zooplankton collection sites (solid line indicates international border between the US and Canada).

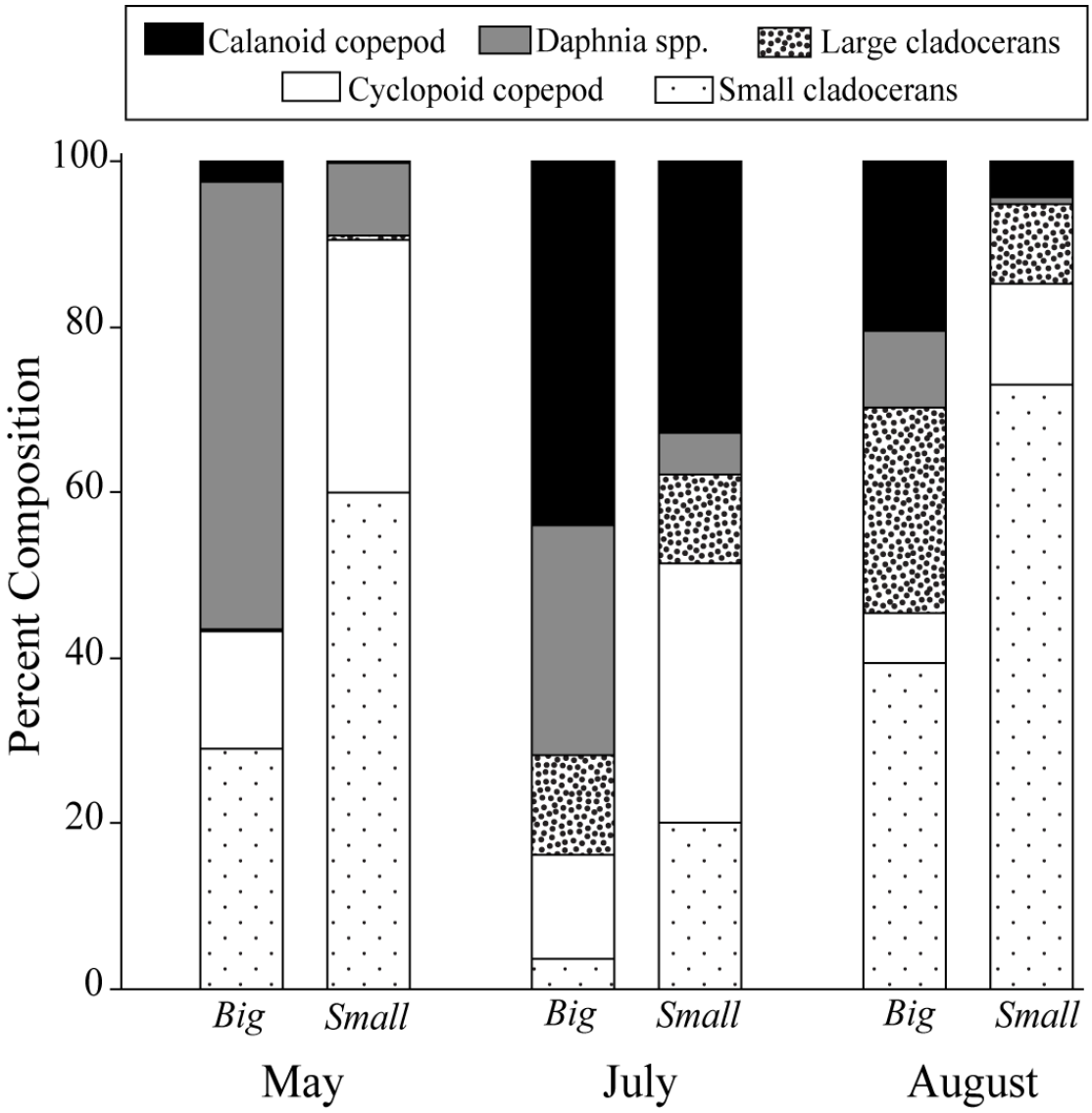

Figure 4.2: Mean percent composition of zooplankton biomass (mg m^{-3}) in the *Big* and *Small* treatment mesocosms (n = 8 of each) on Day 1 of each trial.

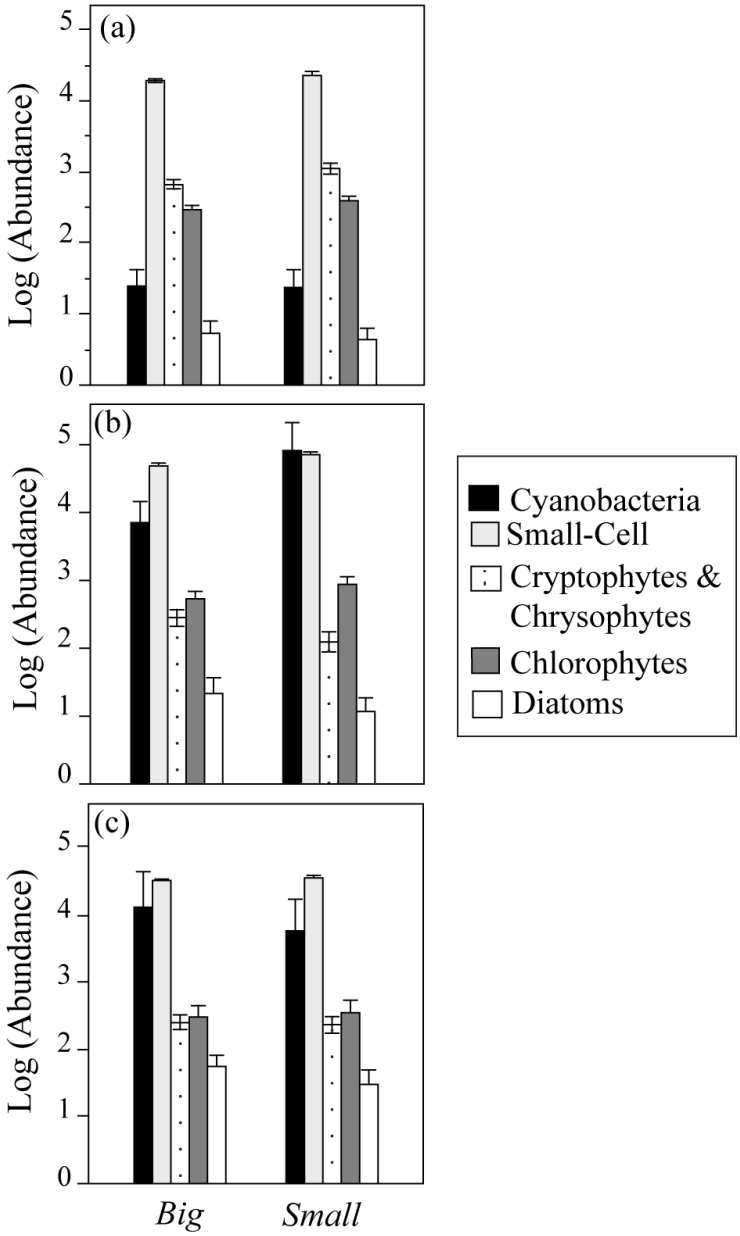

Figure 4.3: Mean log abundance (cells mL^{-1} ± SE) of phytoplankton taxonomic groups in *Big* and *Small* treatments (n = 8 of each) on Day 1 of the (a) May, (b) July and (c) August trials.

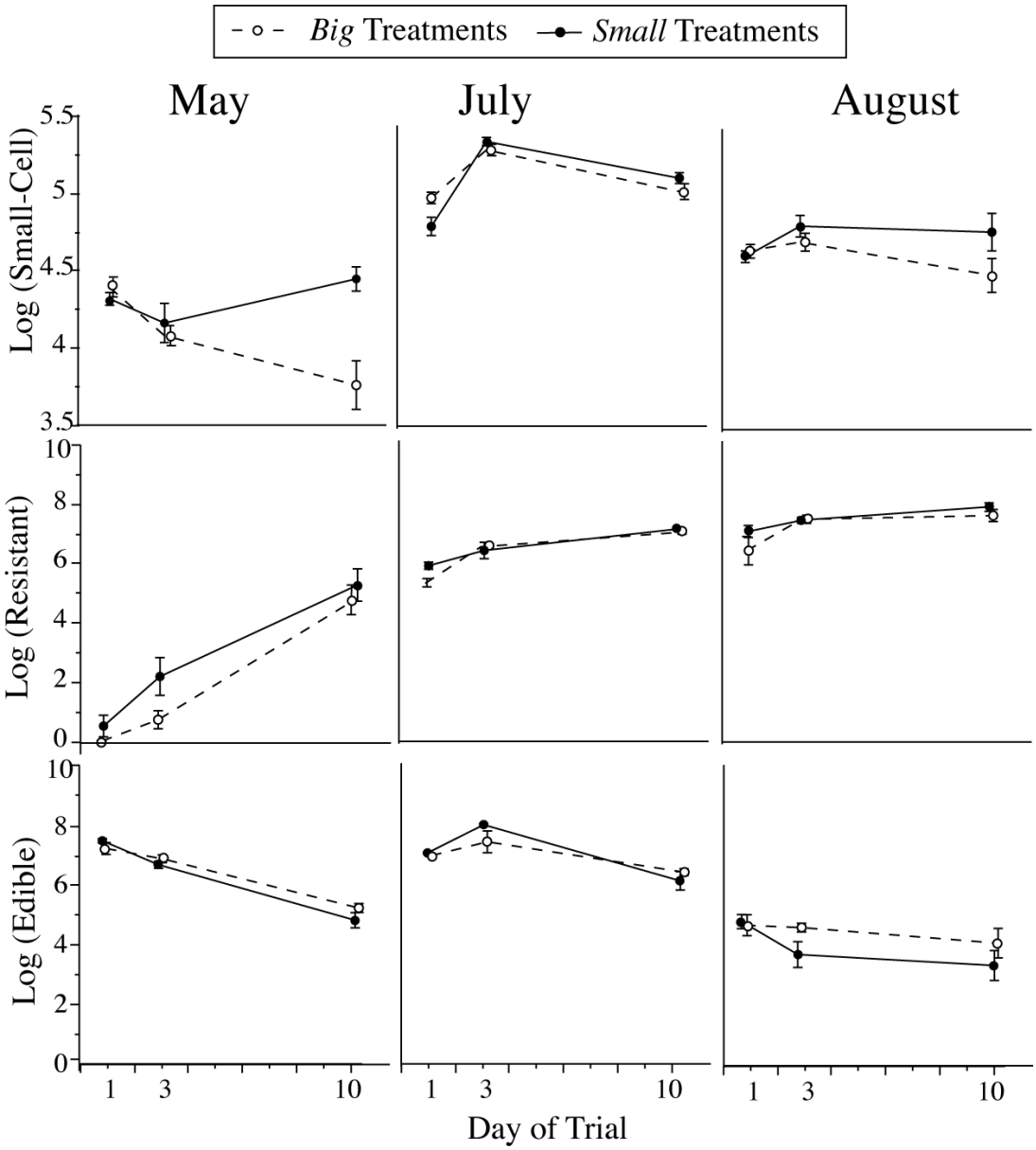

Figure 4.4: Mean log abundance (cells mL^{-1} ± SE) of small-cell phytoplankton, grazing-resistant and edible phytoplankton biovolume (μm^3 mL^1) in *Big* and *Small* treatments (n = 8 of each) on Days 1, 3, and 10 of each trial.

kCHAPTER 5: CONCLUSIONS AND LIMITATIONS

5.1. Introduction

This research was conducted to evaluate the relative roles of nutrient concentrations and trophic dynamics in the development of cyanobacteria blooms. In systems that have recently become eutrophic, the presence of cyanobacteria blooms and trophic perturbations caused by invasive planktivorous fish are indications of substantial degradation of ecological condition (Scheffer *et al.* 1997). The motivation for this research was to gain insight into food web responses to ecosystem-scale changes, using Lake Champlain as a case study.

The goal of this work as a whole was to combine effectively both bottom-up and top-down paradigms in an integrated and comprehensive approach. The studies addressed three specific topics: (1) associations among phytoplankton and nutrient concentration trends over time, (2) the impacts of planktivory by invasive fish on the ambient zooplankton community, and (3) the role of herbivore zooplankton grazers in determining the composition of the phytoplankton community. I sought to link field-based observations with experimentally derived data on mechanisms to better understand the processes that drive cyanobacteria blooms in shallow lake ecosystems. The theoretical and experimental literature on this subject is inconclusive on the exact nature of the role of biotic feedbacks in determining the composition of algal blooms (Elser 1999, Schindler 2006, Paerl and Paul 2012).

I found little evidence of a strong association between nutrient concentrations and phytoplankton community composition in Missisquoi Bay and Saint Albans Bay during cyanobacteria blooms. Invasive white perch (*Morone americana*) and alewife (*Alosa pseudoharengus*) exert selective grazing pressure on large zooplankton in Missisquoi Bay, which has likely contributed to substantial declines in large zooplankton biomass. I used these results to inform the design of my mesocosm study. Results of the manipulation of large zooplankton biomass provided support for the theory that grazing pressure changes the size structure, abundance, and composition of phytoplankton. My results align with mounting evidence (Vanni *et al.* 1997, Elser 1999, Carpenter *et al.* 2001, Hambright *et al.* 2007, Estes *et al.* 2011) that in eutrophic lakes, complex trophic interactions can modify the dynamics of the phytoplankton community and the likelihood of the occurrence of cyanobacteria blooms.

5.2. Limitations

5.2.1. Chapter 2

In my study of long-term nutrient concentration and phytoplankton trends in Missisquoi and Saint Albans bays, I observed substantial inter-annual variation in nutrient concentrations and phytoplankton abundance. I limited my analyses to an evaluation of associations between phytoplankton community composition trends and a small collection of interrelated nutrient variables. There was substantial unexplained variation in the phytoplankton community that I was not able to attribute to nutrients alone. Long-term data regarding the zooplankton community composition, temperature,

or light attenuation profiles could have added more explanatory power to my analyses and allowed me to test more specific hypotheses regarding their role in determining phytoplankton community composition.

The long-term monitoring program dataset that I analyzed was collected with the primary goal of quickly testing for and communicating public health risks related to the presence of cyanotoxins (Watzin *et al.* 2006). A broader monitoring program designed to test for linkages among physical parameters, nutrient concentrations, and trophic dynamics should be based on a conceptual model about how these parameters interact. Monitoring program design and the generation of effective research questions can be aided with a well-articulated ecosystem model (Lindenmayer and Likens 2010). My results provide valuable information from shallow bays in Lake Champlain that can potentially aid in the design of such a program.

For a monitoring program with the goals of detection or prediction of cyanobacteria blooms, fixed sites should be sampled as often as is reasonable, ideally weekly, during the potential bloom development period. The choice of parameters to measure should be focused on those that have been shown to be important in determining phytoplankton community composition. Examples include: dissolved and total nutrient concentrations, light attenuation through the photic zone, zooplankton community composition, and basic water quality measurements (dissolved oxygen, pH, temperature, and conductivity) (Scheffer *et al.* 1997). Recent advances in auto-samplers and optical scanning technology mean that scientists can acquire high-resolution, real time data on nutrient concentrations, phytoplankton, or zooplankton. This is beneficial for both long-

term analyses of ecosystem trends and short term applied uses, such as public notification of health risks associated with toxic blooms.

For the analysis of long-term datasets, multivariate statistical tools can provide estimates of how multiple variables influence fluctuations in community data. Most phytoplankton monitoring datasets are complex and do not fit univariate statistical test requirements of independent predictor variables, normality, and linear responses (ter Braak 1994). Multivariate statistical methods can be used to reduce the number of dimensions in complex datasets and identify influential trends present among years or within a season (McCune and Grace 2002). Several different methods have been valuable for visualizing the interactions among factors that influence phytoplankton community composition and cyanobacteria bloom development in lakes.

Ordination techniques, such as Canonical Correspondence Analysis (CCA) or Redundancy Analysis (RDA), have been used to evaluate relationships among phytoplankton community composition and environmental variables in several types of ecosystems (Laamanen 1997, da Silva *et al.* 2005, Soininen *et al.* 2005). Using these techniques, temperature is often identified as an important environmental explanatory variable in phytoplankton composition (Laamanen 1997, Tian *et al.* 2013).

Nonmetric multidimensional scaling (NMDS) is a nonparametric ordination method that has been used to classify phytoplankton communities, to indicate environmental gradients along which communities are organized, and to determine the similarity of sites with respect to phytoplankton composition or spatial context (ter Braak

1994, Soininen *et al.* 2005, Quinlan and Phlips 2007). Hierarchical clustering and classification techniques have also been used to separate phytoplankton samples over spatial and temporal scales by their compositional or physico-chemical attributes in order to parse out the causes of inter-annual variation in phytoplankton blooms (Kruk *et al.* 2002, McIntire *et al.* 2007), including in Lake Champlain (Pearce *et al.* 2013).

Despite the substantial number of studies that have used multivariate methods, there is no consensus about which factors determine phytoplankton community composition and further studies should be completed (Schindler 2006). Relatively few studies have analyzed long-term time series datasets that combine frequently sampled physical, nutrient, and trophic parameters. This may be a factor that prevents researchers from reconciling conflicting results across different ecosystems. Moving beyond assessments of species composition to connecting drivers with predicted ecosystem changes and testing observed patterns is the next step. Results from long-term analyses can be combined with experimental studies to better predict phytoplankton dynamics and bloom development mechanisms.

5.2.2. Chapter 3

The methods of my diet study were constrained to follow previous methodologies in order to compare current conditions to those described in 2005 (Couture and Watzin 2008). The repetition of previous methods was advantageous for continuity, but led to limitations in assessing the full extent of fish predation pressure on zooplankton and competition between alewife and white perch. My study was not

designed to analyze the grazing pressure of young of year (YOY) white perch and alewife. However, studies of ontogenetic shifts in feeding behavior of both species show that YOY can have substantial influence on zooplankton communities, especially small zooplankton taxa (MacNeill 1990, Stapanian *et al.* 2007). Potentially, competition between these two species, and with native species such as yellow perch, is highest at the YOY stage (Parrish and Margraf 1990, Guzzo *et al.* 2013). A broader study of these interactions could have improved my ability to draw conclusions about implications for the zooplankton community in Missisquoi Bay.

A study of YOY diet composition of alewife and white perch would be valuable to show how ontogenetic shifts in zooplanktivory overlap temporally between the two species. The use of sampling techniques that are more efficient for the collection of juvenile fish would have allowed for a more detailed assessment of diet composition and competition by size class. The degree of overlap in their spawning and juvenile development cycles could make a substantial difference on how these invasive species impact the zooplankton grazer community. YOY alewife are more likely to filter feed than adults and young alewife consume smaller zooplankton than adult alewife (MacNeill 1990, Mills *et al.* 1992). For white perch, the ontogenetic switch from zooplanktivory to benthic invertebrates can occur in very small fish, which adds to their success as invaders (Prout *et al.* 1990). We do not know exactly how YOY alewife and white perch overlap in Lake Champlain.

An additional limitation to my study was the low numbers of alewife collected in 2011, which hindered my ability to come to clear conclusions about their diet

composition or potential interactions with white perch. Unfortunately, 2011 brought record-breaking spring floods to Lake Champlain and was an unusual year for ecological dynamics in the lake. It is possible that alewife were present in Missisquoi Bay, at least during their spawning period that year, as they had been in 2010, but they weren't collected in my sampling efforts. To improve my study, I could have included a larger sampling area, beyond Missisquoi Bay, to better be able to assess interactions between the two species over time.

5.2.3. Chapter 4

The motivation of the original design of my mesocosm study was to analyze responses in the phytoplankton community to manipulations of both the density and size structure of the zooplankton community. Eutrophication and high nutrient concentrations leads to increases in zooplankton density and selective grazing by fish changes the size structure of the zooplankton community but the consequences for the phytoplankton community are not always predictable (Carpenter *et al.* 2001). In hindsight, several improvements to methodology would have increased the chances that I could have executed the original design as planned. If the treatments had been established as intended, my analysis of fixed density and size effects could have indicated how each factor interacts with phytoplankton. These dynamics may play a pivotal role in the development of cyanobacteria blooms (Elser 1999).

A fully factorial, replicated study would have allowed me to test interactions between grazer density and community composition and how they impact phytoplankton.

The blocked design and setup of our mesocosm array functioned basically as planned but the process of collecting zooplankton and transferring them among the treatments introduced more variability than intended and is partly to blame for the treatments not working as planned. There also was substantial mortality in the zooplankton through the sieving processes, which impacted final densities within the mesocosms. While individually counting zooplankton is not practical, gentler methods of separating the size classes and field checks of the densities achieved might have improved the treatment establishment process, particularly for the creation of the "*High*" and "*Low*" zooplankton density treatment levels.

My proposed mesocosm study was to be repeated over the bloom formation period for two years (2011 and 2012) to provide replication over time. However, trial initiation began later than planned because of the spring floods of 2011. Cyanobacteria blooms in Missisquoi Bay began shortly before the first trial started, so I was unable to capture pre-bloom conditions in the 2011 trials. In 2012, I was able to run one successful trial prior to bloom initiation, but succeeding trials were confounded by a diatom bloom and high zooplankton mortality. Replication of more trials over time would have provided data for a more powerful analysis of zooplankton-phytoplankton interactions in Missisquoi Bay.

Artifacts are an additional important concern when analyzing the results of any mesocosm experiment. The degree of their potential impacts on experimental results will depend on sampling times, experimental duration, and mesocosm dimensions (Spivak *et al.* 2011). Artifacts that I observed in my study included a predominance of small-cell

phytoplankton groups and periphyton growth on the sidewalls of the mesocosms. The presence of these artifacts added to the artificial nature of the sampled communities compared to the lake itself, so extrapolation of my results to *in situ* conditions should be done with care. Without explicit testing, it is hard to know exactly how the design of my study and mesocosm artifacts impacted the changes in the zooplankton and phytoplankton densities that I observed.

Elegance in experimental design with sound execution, distinct treatments, and high replication is difficult to achieve. A future study with better treatment creation methods, replication over longer time scales, and the use of larger mesocosms to reduce mesocosm artifact effects could yield better results. After completing my research, I feel that the use of controlled manipulations of zooplankton in mesocosm studies is valuable to better understand the dynamics of phytoplankton. The study of competition and indirect species interactions in multi-species communities using mesocosms will advance our knowledge beyond laboratory-based studies of single species cultures (Gliwicz 1990, Heisler *et al.* 2008). Controlled experiments in settings outside of the laboratory can be informative to compare the relative importance of top-down and bottom-up forces in aquatic ecosystems. However, I have learned that conducting manipulative outdoor experiments with plankton requires extensive planning, especially with regard to treatment establishment, and allowances for flexibility to deal with unpredictable challenges.

5.3. Theoretical Implications and Conclusions

There are constant dynamic feedbacks and interactions between consumers and their resources that determine community structure in both terrestrial and aquatic ecosystems (Power 1992, Polis *et al.* 2000, Carpenter *et al.* 2001). In lakes, consumers impact primary producers and overall ecosystem function by direct predation, alteration of nutrient recycling rates, and changes in biogeochemical processes (Schindler *et al.* 1997, Vanni *et al.* 1997, Estes *et al.* 2011). My results provide support for the importance of cascading trophic interactions in influencing the dynamics of cyanobacteria blooms in shallow bays in Lake Champlain.

Based on my research and observations of the ecosystem, I can conclude that Missisquoi Bay has undergone a state change as a result of several human-caused ecosystem changes including: removal of top predator fish (such as salmonids and walleye), eutrophication, and alien species introductions. Cyanobacteria blooms, high nutrient concentrations, high densities of planktivorous fish, and a shifted size structure of the zooplankton community are all indicators of a lake that has undergone a catastrophic regime shift (Scheffer and Carpenter 2003). My work advances the field by contributing to the understanding of complex food web dynamics in shallow eutrophic bays, including the theory that trophic interactions can be the "final turn" towards dominance by cyanobacteria (Elser 1999).

Moving forward, it is clear that annual patterns of warming and precipitation will change as a result of global climate change and can lead to unpredictable outcomes

for fish, zooplankton, and phytoplankton communities (Paerl and Paul 2012). Future climate change models suggest that cyanobacteria will continue to have advantages over other types of phytoplankton, particularly in shallow lakes as a result of those changes (Scheffer and van Nes 2007, Paerl and Huisman 2009, Kosten *et al.* 2012). The recent climatological and hydrological events of record-breaking flooding and Tropical Storm Irene are examples that I observed firsthand of the types of extreme weather events that are likely continue to impact Lake Champlain. Climate change can lead to changes in ecological forcing factors and to new and unpredictable foodweb structures. My studies provide an incremental addition to our knowledge of how complex trophic interactions can occur. One of the main implications from my research is that shifts in the timing of spring warming may be important to biotic interactions. Grazing by planktivorous fish on large zooplankton and changes in the composition of the phytoplankton community occur over a short time scale each year as the lake warms, and are therefore vulnerable to climactic changes.

There is a need for continued study of cyanobacteria bloom development mechanisms, particularly in cases where potentially toxic blooms threaten the human and ecological health of a lake ecosystem (Scheffer *et al.* 1997, Hyenstrand *et al.* 1998). While short-term successes in reducing eutrophication have been detected from drastic actions such as diverting sewage outflow or stocking high densities of piscivorous fish, long-term prevention or reduction of cyanobacteria blooms requires efforts on multiple fronts over a long time (Schindler 2006). Because of high levels of spatial and temporal

variation in fish, zooplankton, and phytoplankton community composition, more comprehensive analyses of interactions among trophic levels are needed.

In sum total, my research characterizes several aspects of complex trophic dynamics in shallow eutrophic bays of Lake Champlain. My results suggest a focus on more than just nutrient concentrations when evaluating causes of dense annual cyanobacteria blooms in Saint Albans and Missisquoi Bays. Selective grazing by invasive planktivorous fish and shifts in the size structure of the zooplankton grazer community have added to the conditions that favor dominance by cyanobacteria in shallow bays of Lake Champlain. High nutrient concentrations support increased levels of ecosystem productivity, but cascading trophic dynamics are additional forces that are likely contributing to the determination of phytoplankton community composition.

CHAPTER 6: COMPREHENSIVE BIBLIOGRAPHY

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APPENDIX A: ADDITIONAL DATA TABLES FROM MESOCOSM STUDY

In the following pages are several data tables with the zooplankton biomass and phytoplankton response variable data used in evaluation of zooplankton grazing and cyanobacteria bloom development mechanisms (Chapter 4). These date were collected over the course of three 10-day trials (May 2011, July and August 2012).

Table A.1: Mean biomass of zooplankton biomass (mg m^{-3} ± standard error) by major taxonomic group measured in *Big* and *Small* treatment mesocosms (n = 8 of each) throughout each trial.

Trial	Treatment	Day	Calanoid Copepods		*Daphnia*		Large Cladocerans		Cyclopoid Copepods		Small Cladocerans	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
May	*Big*	1	38.3	14.0	836.8	163.9	4.5	1.9	203.6	24.8	400.7	77.4
		3	12.0	3.5	752.0	119.6	8.7	3.5	192.2	18.1	300.1	63.5
		10	2.4	0.4	16.5	3.5	0.1	0.1	52.6	6.4	32.3	7.8
	Small	1	1.5	1.5	70.7	26.2	4.6	1.3	252.8	30.0	510.6	62.1
		3	0.5	0.5	46.8	10.5	0.3	0.3	252.5	29.6	594.8	82.4
		10	3.2	1.1	1.6	0.8	--	--	101.5	13.7	237.7	19.8
July	*Big*	1	39.8	8.2	32.8	10.3	11.4	2.9	7.4	0.6	2.3	0.3
		3	50.8	6.6	19.9	5.6	9.9	3.2	26.9	2.4	8.3	1.3
		10	41.1	6.4	5.0	1.5	10.1	3.0	13.2	2.5	39.1	10.9
	Small	1	9.9	1.4	1.6	0.7	3.4	1.0	10.1	2.5	7.8	3.2
		3	25.0	3.6	1.5	0.8	2.6	1.2	24.2	2.5	12.0	4.3
		10	15.4	3.5	0.8	0.4	3.5	1.2	15.7	4.4	68.6	15.5
August	*Big*	1	66.8	25.0	18.7	5.7	64.8	22.9	7.6	1.2	51.6	12.8
		3	7.7	2.1	1.1	0.4	12.9	4.1	6.1	1.0	67.1	12.9
		10	2.1	1.2	0.7	0.5	6.6	2.8	5.0	1.7	54.3	10.0
	Small	1	3.1	1.0	0.5	0.3	7.2	1.6	12.4	4.5	82.4	33.8
		3	1.4	0.6	--	--	5.6	1.7	11.1	3.3	135.4	54.9
		10	2.1	0.7	--	--	10.9	2.6	13.6	4.4	136.6	29.2

Table A.2: Mean phytoplankton abundance (cells mL^{-1} ± standard error) by major taxonomic group measured in *Big* and *Small* treatment mesocosms (n = 8 of each) throughout each trial.

Trial	Treatment	Day	Cyanobacteria		Small-Cell Groups		Chlorophytes		Diatoms	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE
May	*Big*	1	70	20	19,944	1,597	19	6	343	49
		3	95	65	18,031	5,028	72	30	253	58
		10	473	332	28,249	4,693	1117	527	1881	715
	Small	1	70	24	24,081	2,832	25	9	466	69
		3	52	24	13,235	1,698	85	37	280	45
		10	187	42	8,942	2,169	149	39	431	117
July	*Big*	1	1,213	238	54,488	5,670	122	33	831	278
		3	2,892	457	143,680	6,901	1207	218	3440	328
		10	2,163	917	91,977	5,464	550	105	2189	331
	Small	1	1,850	454	73,575	4,833	93	22	1416	314
		3	2,077	272	131,890	9,289	912	148	2983	428
		10	1,747	328	84,336	9,147	503	93	1552	256
August	*Big*	1	20,200	8,802	34,155	2,327	230	76	949	275
		3	12,080	3,665	53,803	5,801	390	104	890	279
		10	8,338	4,008	58,119	11,051	460	69	1120	187
	Small	1	4,099	1,428	38,920	2,889	118	24	1000	427
		3	8,802	2,768	42,622	4,393	359	136	726	135
		10	7,274	2,482	31,631	6,053	270	106	2390	1338

Table A.3: Mean phytoplankton biovolume (μm^3 mL^1 ± standard error) of phytoplankton edibility groups, generic richness and Shannon diversity index measured in *Big* and *Small* treatment mesocosms (n = 8 of each) throughout each trial.

Trial	Treatment	Day	Grazing-resistant		Edible		Richness		Diversity	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE
May	*Big*	1	20,166	1,637	8,066	900	9.9	0.7	0.36	0.02
		3	18,236	5,037	4,662	1,317	10.2	0.7	0.39	0.04
		10	30,389	4,181	1,547	319	17.0	0.8	0.52	0.04
	Small	1	24,278	2,828	9,520	1,184	10.0	0.4	0.37	0.01
		3	13,400	1,693	3,974	765	10.4	0.6	0.36	0.03
		10	9,369	2,276	606	166	17.1	1.1	0.49	0.03
July	*Big*	1	58,200	5,845	4,679	196	15.0	0.5	0.33	0.02
		3	156,065	7,248	19,998	2,088	17.6	0.7	0.35	0.01
		10	106,421	6,176	3,650	455	17.1	0.5	0.41	0.01
	Small	1	76,924	5,045	5,343	139	14.7	0.2	0.25	0.01
		3	140,850	9,601	17,791	1,149	17.4	0.7	0.34	0.01
		10	96,817	9,754	3,649	516	17.9	0.8	0.41	0.03
August	*Big*	1	61,261	10,882	1,904	236	12.3	0.4	0.41	0.02
		3	74,075	9,270	1,339	217	14.0	0.7	0.42	0.03
		10	91,481	16,946	2,003	507	13.5	0.6	0.49	0.02
	Small	1	49,155	2,911	1,686	91	12.4	0.4	0.35	0.04
		3	58,670	6,849	1,398	160	13.7	0.7	0.40	0.03
		10	53,345	6,753	3,543	1,390	11.4	0.8	0.53	0.03